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DYNAMICS OF A MIGRATORY FISH POPULATION WITH APPLICATIONS TO THE MANAGEMENT OF SABLEFISH IN THE NORTHEAST PACIFIC OCEAN

A

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of the University of Alaska Fairbanks

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By

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DYNAMICS OF A MIGRATORY FISH POPULATION WITH APPLICATIONS TO THE MANAGEMENT OF SABLEFISH IN THE NORTHEAST PACIFIC OCEAN

By

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Abstract

Quantitative models are developed to describe the dynamics of an age-structured migratory fish population subject to exploitation. Migration rates are quantified, alternatives ways of apportioning harvest among areas are examined, and the dynamics of a migratory population is described within the general theoretical framework of a projection matrix model. Application of these modeling efforts is within the context of the sablefish (*Anoplopoma fimbria*) fishery in the North Pacific Ocean.

A Markov model that includes natural and fishing mortality, tag reporting and shedding rates, and migration is used to quantify migration rates of tagged sablefish among fishery regulatory areas. Estimates of annual migration rates out of an area are in the range 19-69% for small (< 57 cm fork length (FL)), 25-72% for medium (57-66 cm FL), and 27-71% for large (> 66 cm FL) sablefish. The predominant direction of migration along the continental slope is eastward for large sablefish and westward for small sablefish. Most estimates of migration are precise, unconfounded, and robust to perturbations of input constants.

An age-structured model that includes migration is constructed to examine harvest policies for sablefish. Areal estimates of yield-per-recruit depends on the geographic distribution of recruitment. In general, when evaluated under the current annual exploitation rate of 10%, apportioning harvest among areas based on areal estimates of biomass and apportionment based on the steady-state distribution of biomass give similar results. A policy of apportionment based on a weighted moving average of areal estimates of available biomass is preferred to others. This policy adapts to current information about geographic distribution of biomass, reduces the effects of measurement error, and does not require estimates of migration probabilities for implementation.

The reproduction, mortality and migration of an age-structured fish population are incorporated into a projection matrix model. The model is parameterized to include areal specificity in the stock-recruitment relationship and events such as larval dispersion that is decoupled from local reproduction. For the sablefish fishery where direction of movement is age dependent, fishing at a common rate among areas may be detrimental to the population in a given area. Area-specific fishing strategies can be devised to meet management objectives such as maintenance of areal spawning potential.

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Acknowledgments

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Introduction

Many populations of fish display some form of movement or migration that influences their spatial distribution. Movement can generally be considered as any change in the location of individuals of a population. Migration is a type of movement pattern that has disparate definitions in the literature. Migration was defined by Heape (1931) and Harden Jones (1968) as "a class of movement which impels migrants to return to the region from which they have migrated." The word "impel" is used in the sense of biological necessity and no distinction is made between passive and active migrations (Harden Jones, 1968). Quinn and Brodeur (1991) used the definition of migration as "movements of individuals coordinated in space and time.....not necessarily accompanied by a return movement and are often repeated throughout the lifetime of an organism". Regardless of the definition it may be difficult to distinguish whether a movement pattern is migratory in the sense of a return to the region of origin as defined by Heape (1931) and Harden Jones (1968), and the terms movement and migration are often used synonymously.

Migration may be related to spawning, environmental conditions, feeding, and transitions between life history stages. Such movements may occur during many phases of the life history of a fish such as passive movements during a pelagic larval phase or more active migrations of adults related to spawning or feeding. For some marine fishes, adult movement patterns appear to compensate for larval dispersion patterns. Some examples of fish that undergo significant migrations are Pacific halibut (*Hippoglossus stenolepis*), Pacific whiting (*Merluccius productus*), sablefish (*Anoplopoma fimbria*), tunas (i.e., *Thunnus* spp.), anadromous salmonids (*Oncorhynchus* spp. and *Salmo* spp.), herrings (*Clupea* spp.), cods (*Gadus* spp.), plaice (*Pleuronectes platessa*), and eels (*Anguilla* spp.).

Harden Jones (1968) classified the movement/migration of fishes into three categories; spawning, feeding, and wintering that often result in predictable seasonal changes in spatial distribution. These three categories are linked to a fish's life cycle and there may be considerable overlap and interactions among the categories. For example, wintering migrations may coincide with spawning migrations, and migrations from near shore nursery areas to offshore areas are usually related to a transition from the juvenile to adult life stage. Examples of spawning migrations include movement to deeper water exhibited for many Pacific Ocean flatfish species (Alverson, 1966), the homing to natal spawning areas of anadromous fishes, and the offshore spawning aggregations of Atlantic cod (*Gadus morhua*; Rose *et al.*, 1995). Feeding migrations are often in the opposite direction of spawning migrations as is the case for Pacific whiting (Swartzman *et al.*, 1987) and Atlantic cod (Rose *et al.*, 1995). Migrations may be highly variable and depend on location of prey and environmental conditions as is the case for the migrations of yellowfin tuna (*Thunnus albacares*; Deriso *et al.*, 1991), and Atlantic cod (Kulka *et al.*, 1995). Examples of wintering migrations are the latitudinal shifts of many Mid-Atlantic Ocean fishes (e.g., bluefish [*Pomatomous saltatrix*]) related to seasonal changes in water temperature (Tyler, 1971; Colvocoresses and Musick, 1983). Some migration patterns defy such narrow classification. For example, no particular spawning or feeding grounds are known to exist for sablefish. For this species, there is a general directional migration pattern that is age dependent but fish of the same age and size may at times be migrating in opposite directions (Sasaki, 1985; Fujioka *et al.*, 1988). This migration pattern may compensate for dispersal of larval stages. In addition, there appears to be considerable intra-specific variation: a portion of the population migrates, sometimes long distances, while another portion is sedentary.

From the perspective of fisheries management, knowledge of movement patterns is useful for examining stock structure, for assessment of anthropogenic influences on fish populations such as fishing and pollution, and to assess alternative harvest strategies.

For example, examination of the relationship between movement patterns and geographic distribution may allow identification of an optimal geographic apportionment of harvest that maximizes sustainable yield and economic returns from a fishery.

Although the importance of migration was recognized as early as 1902 by the International Council for the Exploration of the Sea (Arnold, 1995) and by Beverton and Holt (1957) who described some theoretical methods for estimating exchange rates among geographic areas, migration is frequently a life-history trait that is not included when describing the dynamics of exploited fish populations. This may be partly due to the added complexity that migration adds to population models. Also for many populations, migration behavior has not been sufficiently quantified, and for others data may not be available to quantify migration. However, for fisheries that occur in different geographic areas, are prosecuted by different user groups, and in some instances may cross international boundaries, knowledge of how a fishery in one area interacts with another may lead to improved management (e.g., Swartzman *et al.*, 1987).

While few studies have examined the implications of migration for the management of commercial fisheries, there has been a surge in recent years of studies focusing on development and application of quantitative methods for assessing and characterizing migratory fish populations. For example, a general framework has been developed for estimating movement rates among geographic areas from tag data (Ishii, 1979; Hilborn, 1990). A theoretical model of the geographic range and distribution of marine fish populations has been applied to maximizing sustainable yield (MacCall, 1990). Migration rates have been integrated with catch-at-age analysis and applied to Pacific halibut (Quinn *et al.*, 1990). Dispersal and migration of a fish population has been incorporated into a simulation model of stock and fleet dynamics (Hilborn and Walters, 1987). Areas closed to fishing as a management tool were evaluated within the context of a migratory population (Polacheck, 1990). Movement rates estimated via a diffusion model were applied to yield-per-recruit analysis of yellowfin tuna (Deriso *et al.*,

1991). A recent issue of the *ICES Journal of Marine Science* (ICES, 1995) was devoted to the description, assessment, and mangement of migratory fishes of the North Atlantic Ocean.

This thesis primarily focuses on describing the population dynamics of a migratory fish population subject to exploitation. The thesis starts first with the quantification of migration rates among fishery regulatory areas from tagging data by using the method of Hilborn (1990). The model structure is described, parameters are estimated via maximum likelihood, and the sensitivity to input constants is explored. Next, the estimated migration rates are incorporated into a simulation model to evaluate alternative ways of apportioning harvest among areas, an important topic that surprisingly few studies have addressed. Finally, the population dynamics of an exploited, migratory fish population is put within the general theoretical framework of a projection matrix model. The model in its most general form is described by Caswell (1989) but without development of the formulation for an exploited fish population that enables evaluation of harvest strategies.

The impetus for this study originated in the need to quantify migration rates and to examine harvest strategies for sablefish, a highly migratory, slow-growing, long-lived, demersal fish of the continental slope of the North Pacific Ocean. Thus, the illustration of the methods for describing a migratory fish population is done with sablefish data. One of the deepest-dwelling commercially valuable species in the northeastern Pacific Ocean, sablefish has been the target of domestic and foreign fisheries since the end of the last century (Sasaki, 1985; McDevitt, 1986). With the advent of 200-mile fishing zones in 1977, US and Canadian domestic fisheries for sablefish replaced foreign fisheries dominated by Japan. Most of the catch now comes from waters off Alaska managed by the North Pacific Fishery Management Council (NPFMC) (McDevitt, 1986), and is exported to Japan (Miller, 1986). Since 1995, the fishery for sablefish in Alaska has been managed by individual transferable fishing quotas (IFQs) on an areal basis. Under this

management system, an individual owns the right to a certain portion of the catch limit within an area. Thus, apportioning the catch limit among areas can have important social and economic effects.

Each of the following chapters are presented in the form of a separate manuscript. Chapter 1 has been published, chapter 2 has been accepted for publication (i.e., in press), and chapter 3 is to be submitted for publication. Note that some of the equation notation has been altered from the original manuscripts to assure consistency among the chapters. In addition, there are some minor changes in the text from the original manuscripts based on suggestions of reviewers of this thesis.

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Chapter 1.

Movement Dynamics of Tagged Sablefish in the Northeastern Pacific[1]

Abstract

We used a Markov model to quantify movement rates of tagged sablefish (*Anoplopoma fimbria*) among regulatory areas of the North Pacific Fishery Management Council during 1979-1987. The model included natural and fishing mortality, tag reporting and shedding rates, and movement probabilities. Maximum likelihood was used to estimate the parameters of the model. Estimated annual movement rates out of an area were in the range 19-69% for small (less than 57 cm fork length (FL)), 25-72% for medium (57-66 cm FL), and 27-71% for large (more than 66 cm FL) sablefish. The predominant direction of movement along the continental slope was eastward for large sablefish and westward for small sablefish. Most estimates of movement rates were precise, unconfounded, and robust to perturbations of input constants (natural and fishing mortality, and tag reporting rates), except for some imprecise estimates of large sablefish. The results indicate that movement plays an important role in determining the amount of sablefish available for harvest in an area. To account for the interactions among fisheries in different areas, the movement dynamics of sablefish should be incorporated into a stock assessment based on size or age-structure.

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[1]An earlier version of this chapter is Heifetz, J. and Fujioka, J.T. 1991. Movement dynamics of tagged sablefish in the northeastern Pacific. Fisheries Research 11:355-374.

Introduction

Sablefish (*Anoplopoma fimbria*) is a slow-growing, long-lived, demersal fish of the continental slope of the North Pacific. One of the deepest-dwelling commercially valuable species in the northeastern Pacific, its populations have been the target of domestic and foreign fisheries since the end of the last century (Sasaki, 1985; McDevitt, 1986). With the advent of 200-mile fishing zones in 1977, US and Canadian domestic fisheries for sablefish replaced foreign fisheries dominated by Japan. Most of the catch now comes from waters off Alaska managed by the North Pacific Fishery Management Council (NPFMC) (McDevitt, 1986), and is exported to Japan (Miller, 1986). The 1989 catch of 34,200 t from waters off Alaska had an ex-vessel value of $62 million (Pacific Fishery Information Network, 1990), making sablefish one of the most valuable and sought-after species in the region.

The US fishery in the northeastern Pacific is managed by discrete geographic areas. Harvest strategies include annual catch quotas that are typically apportioned among fishery regulatory areas in direct proportion to geographic distribution of biomass (Fujioka, 1989). Tagging experiments indicate that sablefish move among regulatory areas (Beamish and McFarlane, 1988; Fujioka *et al.*, 1988). This movement of fish among areas should be considered in any alternative to the current strategy of apportionment. The importance of movement in the population dynamics of sablefish needs to be determined to devise more appropriate harvest strategies.

In this paper, we quantify annual movement rates of sablefish among fishery regulatory areas by using the method of Hilborn (1990) to describe the movement, survival, and recovery of tagged sablefish. We estimate movement rates by maximizing the likelihood of observed tag recoveries. We also identify sources of uncertainty and determine their effect on estimated movement rates.

Methods

Tag Release and Recovery Data

We used tag releases from the 1979-1987 Japan-US cooperative longline survey (hereafter referred to as the "longline survey"; Sasaki, 1985) and recoveries from 1979 to 1987. Although various agencies and countries have tagged sablefish throughout the North Pacific (Fujioka *et al.*,1988), only the release of fish from the longline survey occurred at stations equidistantly spaced along the continental slope throughout the area of the NPFMC (Figure 1.1).

From 1979 to 1987, more than 128,000 sablefish of exploitable size (more than 40 cm fork length (FL)) were tagged and released using the methods of Sasaki (1985). Fish were tagged with individually numbered floy anchor tags. For each tagged fish, release location and fish length were recorded. Tag releases were multiplied by 0.90 to account for immediate shedding of tags (Beamish and McFarlane, 1988). As of 1987, approximately 4,700 tagged fish were recaptured and reported. Of these tag returns, about 4,300 had useful recovery area information. An example of release and recovery data is given in Table 1.1. Recoveries have been from the five NPFMC regulatory areas, as well as from British Columbia (BC) and the West Coast of the US (WC) (Figure 1.1). Tags were recovered mostly by commercial fishing or processing operations, with a few recoveries from research cruises (less than 1% of the total recoveries).

Model Description

Hilborn's (1990) method is a general modeling approach rather than a packaged model. Thus, we give sufficient detail with respect to underlying assumptions, sources of error, and mathematical formulations. The method has four major components: (1) a population dynamics and movement model, (2) an observation model, (3) a likelihood specification, and (4) a nonlinear function minimization procedure.

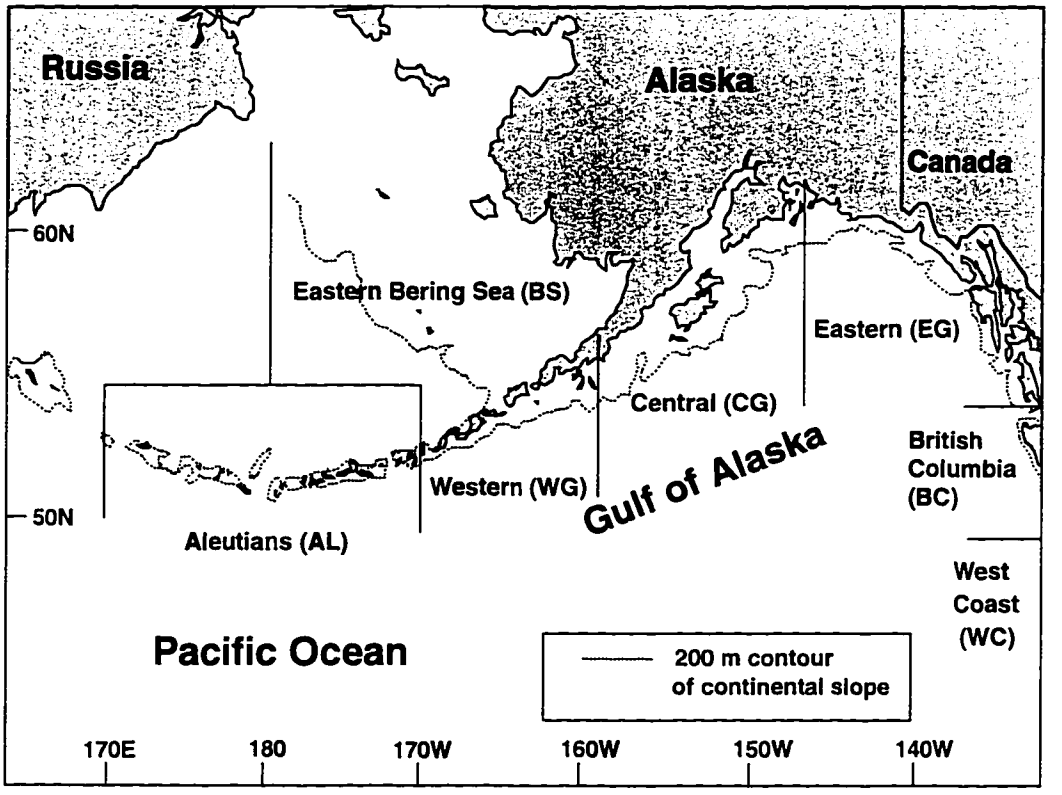

Figure 1.1. Northeast Pacific Ocean showing North Pacific Fishery Management Council (NPFMC) regulatory areas, British Columbia, and the West Coast Coast of the USA. Tagged sablefish for this study were released from 108 equally spaced stations throughout the area of the NPFMC along the continental slope. Abbreviations for areas that are used throughout the text are in parentheses.

Table 1.1. Example of release and recovery data for three length groups of tagged sablefish. Data are for sablefish tagged in the Central Gulf of Alaska during 1980. *n* = number of tag releases.

Recovery area	Recovery year							
	80	81	82	83	84	85	86	87
Small (< 57 cm FL), n=1397								
WC	0	0	0	0	0	0	0	0
BC	0	0	0	0	0	1	1	0
EG	0	0	0	2	3	2	3	0
CG	5	3	2	5	4	4	2	1
WG	0	2	2	0	0	3	0	0
BS	0	2	1	0	0	0	0	0
AL	0	0	0	1	0	0	2	0
Medium (57-66 cm FL), n=1744								
WC	0	0	1	0	0	0	0	0
BC	0	0	1	2	3	1	0	1
EG	0	3	4	5	5	5	4	1
CG	8	9	7	3	10	6	4	1
WG	1	0	2	0	1	0	0	0
BS	0	0	0	0	0	0	0	0
AL	0	0	0	1	0	0	0	0
Large(>66 cm FL), n=853								
WC	0	0	1	0	1	0	0	0
BC	0	7	3	5	3	1	0	0
EG	1	4	3	2	1	3	0	0
CG	3	7	2	2	4	3	1	0
WG	0	0	0	1	0	0	0	0
BS	0	0	0	0	0	0	0	0
AL	0	0	0	0	0	0	0	0

BC, British Columbia; EG, Eastern Gulf of Alaska; CG, Central Gulf of Alaska; WG, Western Gulf of Alaska; BS, Eastern Bering Sea; AL, Aleutians.

Earlier studies have shown that the pattern of sablefish movement is related to fish length (Bracken, 1982; Fujioka *et al.*, 1988). Accordingly, separate models are fitted and results compared between different length groups of released fish: small (less than 57 cm FL), medium (57-66 cm FL), and large (more than 66 cm FL) sablefish. This stratification reflects both age and sex differences. Females grow faster and mature at a larger size than males (Sasaki, 1985). At 57 cm FL, half the male sablefish in the Gulf of Alaska are mature and at 67 cm FL half the female sablefish are mature (Sasaki, 1985). Thus, immature fish predominate in the small-length group, and mature fish predominate in the large-length group.

Population Dynamics and Movement Model

This model component describes how tagged fish from a release group survive and move over time. A release group is defined as fish released into NPFMC regulatory area i in year t. We assume that survival is independent of movement and affected by instantaneous annual rates of natural mortality M, fishing mortality $\lambda f_{t,i}$, and tag loss H. The values for M, H, and $\boldsymbol{f}$ are constant, where $\boldsymbol{f}$ is the set of the $\{f_{t,i}\}$. The calibration parameter λ accounts for bias in assumed values for $\boldsymbol{f}$ and is estimated separately for each length group. Using the basic fisheries mortality model (Ricker, 1975), we let $\boldsymbol{S}_{m,t}$ be a diagonal matrix of survival rates in each area during month m of year t, where the i^{th} element of $\boldsymbol{S}_{m,t}$ is described by

$$S_{m,t,i} = \exp\left\{\frac{-[\lambda f_{t,i} + M + H]}{12}\right\}. \qquad (1.1)$$

Sablefish were usually tagged from May to September in the longline survey. On average, these fish were vulnerable to fishing and natural mortality for half a year during the year of release. Equation (1.1) is modified to account for the proportion of fishing mortality $U_{t,i}$ that occurred after fish were released and a half a year of natural mortality

$M/2$ and tag loss $H/2$. The monthly survival rate of tagged fish during this 6-month period $S'_{a,m,t}$ is described by

$$S'_{m,t,i} = \exp\left\{\frac{-\left[U_{t,i}\,\lambda f_{t,i} + \frac{M}{2} + \frac{H}{2}\right]}{6}\right\}.$$

We let Θ be a matrix of annual probabilities of movement where the i,k^{th} element of Θ ($\theta_{i,k}$) is the annual probability of movement from area i to area k. We reparameterize Θ in terms of monthly probabilities of movement Φ, such that Φ^{12} equals Θ. Movement is assumed to occur instantaneously at the end of a month. The row vector of abundance of release group g in each area at the beginning of a year $N_{g,t+1}$ is then the function of prior abundance $N_{g,t}$, survival $S_{m,t}$, and movement Φ

$$N_{g,t+1} = N_{g,t}(S_{m,t}\Phi)^{12} \qquad (1.2)$$

In the year of release, $S'_{m,t}$ is substituted for $S_{m,t}$, and the exponent six is substituted for 12.

The i,k^{th} element of Φ ($\phi_{i,k}$) is the probability of a fish moving from area i to area k at the end of a month m, and is described by

$$\phi_{i,k} = \frac{\rho_{i,k}}{\rho_i}\left\{1 - \exp[-\rho_i]\right\} \qquad \text{for } i \neq k$$

$$\phi_{i,k} = \exp[-\rho_i] \qquad \text{for } i = k$$

$$\rho_{i\cdot} = \sum_{i \neq k} \rho_{i,k} \,.$$

The $\rho_{i,k}$ values are the movement parameters to be estimated and are analogous to instantaneous rates. By constraining the $\rho_{i,k}$ values to be non-negative, this parameterization lets Φ and Θ have the properties of a Markov transition matrix; the row sums equal unity and all the elements are non-negative (Bharucha-Reid, 1960). A movement process is Markovian if the probability of a fish moving from area i to area k at the end of a month depends only on the area i the fish is in at the beginning of the month. Thus, movement of fish is modeled as a discrete monthly event where all fish in an area have the same movement probabilities independent of their previous history.

The model is formulated with monthly parameters to reduce the number of parameters that need to be estimated and to approximate the survival and movement process with a simple formulation. Fish that move are assumed to move to a contiguous management area in one month. This assumption reduces the number of movement parameters that need to be estimated (Hilborn, 1990). We believe this assumption is approximately correct because no tag returns came from a non-contiguous area during the month after release. Thus, at the end of a month, a fish in an area can either remain in that area or move to a contiguous area. Description of the population dynamics and movement model in annual steps requires a more complicated formulation with more parameters to account for movement to non-contiguous areas, the possibility of returning to the previous area, and survival along the way.

Observation Model

The second model component adapts the Baranov catch equation (Ricker, 1975) to describe the recovery and reporting of tagged fish. The number of tag recoveries $Q_{g,t,i}$ from a release group in an area/year stratum is obtained from the product of fishing mortality $\lambda f_{t,i}$, the tag reporting rate W_i, and the average abundance of tagged fish $\bar{N}_{g,t,i}$

$$Q_{g,t,i} = \bar{N}_{g,t,i} \lambda f_{t,i} W_i \,. \qquad (1.3)$$

Fishing mortality is multiplied by $U_{t,i}$ in the year of release. An approximation to $\bar{N}_{g,t,i}$ is the number of tagged fish in each area at the midpoint of a year. Equation (1.2) can be modified to give

$$\bar{N}_{g,t} = N_{g,t}(S_{m,t}\Phi)^6 \ .$$

The exponent six represents the midpoint of the year. In the year of release, $S'_{m,t}$ is substituted for $S_{m,t}$, and the exponent three (the midpoint of the remainder of the year) is substituted for six.

Likelihood of Recoveries

The third model component specifies the likelihood (L) of the predicted number of tag recoveries $\boldsymbol{Q}$ given the observed number of tag recoveries $\boldsymbol{R}$

$$L(\boldsymbol{Q}|\boldsymbol{R}) = \prod_g \prod_t \prod_i L[Q_{g,t,i}|R_{g,t,i}] \ . \qquad (1.4)$$

Following Hilborn (1990), if we assume the sampling distribution of tag recoveries is approximated by the Poisson distribution, then

$$L[Q_{g,t,i}|R_{g,t,i}] = \frac{\exp(-Q_{g,t,i})Q_{g,t,i}^{R_{g,t,i}}}{R_{g,t,i}!}$$

An assumption of the Poisson distribution is that there is a low probability of any individual tag being recovered in any area/time stratum. Alternatively, the multinomial distribution is often used in the analysis of tagging data (Seber, 1982). Hilborn (1990) showed that the multinomial and Poisson approaches give nearly identical answers when

the probability of capture is low and he recommended that computational convenience should govern the choice of method. Thus, based on the low proportion of tags recovered (4%), we assume that the sampling distribution of tag recoveries is approximated by the Poisson distribution.

Nonlinear Optimization

The final model component is a nonlinear optimization computer program that maximizes the likelihood of $\boldsymbol{Q}$ given $\boldsymbol{R}$. The matrix $\mathbf{Q}$ which maximizes equation (1.4) is a function of the maximum likelihood estimates of the model parameters ($\rho_{i,k}$ values and λ). We used the GAUSS program MAXMUM (Edlefsen, 1986), which minimizes an objective function with respect to a set of parameters. For our study, the objective function was the negative $\log_e$ of equation (1.4), i.e.-$\log_e L$. Output from this program includes maximum likelihood estimates of parameters, standard errors, and *t*-statistics. Modifications of MAXMUM were made to obtain parameter correlation coefficients. Estimated standard errors and correlations were obtained from the inverse Hessian matrix (Bard, 1974). Convergence was usually obtained in less than 4 h on a 386/16 MHZ microcomputer.

The estimates of standard errors of the monthly movement parameters ($\rho_{i,k}$ values) do not directly provide estimates of the standard errors of the annual movement probabilities $\boldsymbol{\Theta}$. We use the parametric bootstrap to estimate standard errors of $\boldsymbol{\Theta}$ (Efron and Tibshirani, 1986) because derivation of the standard errors of $\boldsymbol{\Theta}$ via the delta method (Seber, 1982) was too difficult. Direct bootstrapping of the tag data and calculation of parameter estimates was impractical because of the computation time required (4 h per convergence). Instead, we used the multivariate normal distribution as a large sample approximation to the joint sampling distribution of the $\rho_{i,k}$ values. Given estimates of $\rho_{i,k}$ values, replicated sets $\rho^*_{i,k}$ values were drawn from the multivariate normal distribution having the same mean vector and variance-covariance matrix as the estimated $\rho_{i,k}$ values

(Scheuer and Stoller, 1962; Naylor *et al.*, 1966). Four hundred sets of $\rho^*_{i,k}$ values were generated. These replicated sets were then converted to $\theta^*_{i,k}$ values. The standard deviation for each $\theta_{i,k}$ was calculated from the distribution of each $\theta^*_{i,k}$ in the usual way. The standard deviation is an estimate of the standard error of the annual movement probabilities.

Following Hilborn (1990), we examined the fit of our model to observed tag returns by using the "deviance" of McCullagh and Nelder (1983). The deviance for any observation is

$$deviance_{g,t,i} = -2\left\{\log_e L[Q_{g,t,i}|R_{g,t,i}] - \log_e L[R_{g,t,i}|R_{g,t,i}]\right\}$$

A large value indicates a poor fit of the model to an individual data point. An overall goodness-of-fit statistic for testing the adequacy of the fitted model can be based on the χ^2 distribution using the $\sum deviance_{g,t,i}$ as a test statistic.

A likelihood ratio test was used to compare the results from the three length groups (Wilks, 1962). The null hypothesis was that a reduced model with common parameters for each length group was identical to a full model with separate parameters for each length group.

Model Application

Baseline Analysis

For reliable estimation, tagging and recapture should take place in all geographic strata (Hilborn, 1990). In the longline survey, tagging did not take place outside the area of the NPFMC which consists of the West Coast of the USA (WC) and British Columbia (BC). Very few tags (0.9%) have been recovered in WC; therefore, we assume that movement of tagged fish to WC was negligible and eliminated its two parameters. We could not make this assumption for BC because considerable numbers of tags (8.6%) were recovered in BC. We constrain the movement probability from BC to the Eastern

Gulf of Alaska (EG) to be equal to zero (i.e., $\rho_{BC,EG} = 0$) to circumvent this problem. This constraint is analogous to assuming that once a tagged fish from EG moves to BC it does not return. Thus, there are 12 parameters (11 $\rho_{i,k}$ values and λ) to estimate for each length group.

We incorporated auxiliary information to determine appropriate values for the constants, f, U, W, M and H. Table 1.2 shows the f used in the model. The $f_{t,i}$ for area i during year t is obtained from

$$f_{t,i} = \frac{C_{t,i}}{\bar{B}_{t,i}} \qquad (1.5)$$

where $C_{t,i}$ is the catch and mean exploitable biomass $\bar{B}_{t,i}$ is

$$\bar{B}_{t,i} = B_{\text{GOA.84}} \left| \frac{RPW_{t,i}}{RPW_{\text{GOA.84}}} \right| .$$

Table 1.2. Input values for $f_{t,i}$ values used in the model.

Area	Year								
	1979	1980	1981	1982	1983	1984	1985	1986	1987
BC	0.071	0.076	0.062	0.070	0.088	0.088	0.062	0.036	0.034
EG	0.100	0.071	0.060	0.045	0.058	0.064	0.054	0.073	0.067
CG	0.038	0.051	0.055	0.027	0.029	0.031	0.023	0.051	0.067
WG	0.038	0.057	0.047	0.026	0.021	0.021	0.021	0.042	0.046
BS	0.020	0.032	0.037	0.045	0.062	0.026	0.018	0.027	0.078
AL	0.012	0.004	0.008	0.012	0.007	0.009	0.010	0.025	0.032

BC, British Columbia; EG, Eastern Gulf of Alaska; CG, Central Gulf of Alaska; WG, Western Gulf of Alaska; BS, Eastern Bering Sea; AL, Aleutians.

$B_{GOA.84}$ is the 1984 Gulf of Alaska (GOA) trawl survey biomass estimate from 200 to 1000 m, and $RPW_{t,i}$ values are the relative population weights from the longline survey (Fujioka, 1989; Sigler, 1989; McDevitt, 1990). In BC, $B_{t,i}$ is assumed equal to $B_{t,i}$ in EG because no biomass estimates were available for BC. We have assumed in eqn. (5) that the mean weight of fish in the commercial catch is the same as in the trawl survey. This assumption was probably not seriously violated because most of the commercial fishery occurred over the same depth range as used in calculation of $B_{t,i}$. Fish weight information was not available from the commercial fishery to evaluate this assumption. The values used for f are subject to various sources of error, and f is likely to differ by length category. The parameter λ is estimated separately for each length group to allow for bias in f.

The proportion of fishing mortality $U_{t,i}$ that occurred after fish were released is obtained from

$$U_{t,i} = \frac{C'_{t,i}}{C_{t,i}}$$

where $C'_{t,i}$ is the catch taken after the midpoint of a year (Pacific Fishery Information Network, 1990) .

Reporting rates W may depend on area and year. In our application, sufficient information was available to evaluate reporting rates by two broad geographic areas but not by year. The reporting rate in the area of the NPFMC ($W_{NPFMC} = 0.24$) is computed by comparing the number of tag recoveries from the longline survey with the number of tag recoveries from the commercial fishery. If all tags recovered in the longline survey are reported (a reasonable assumption), then an estimate of W(NPFMC) is

$$W_{NPFMC} = \frac{G_{fishery}}{G_{survey}}$$

$G_{fishery}$ is the ratio of number of tags recovered in the fishery to the total catch in the fishery, and G_{survey} is the ratio of number of tags captured in the longline survey to total catch in the longline survey. Almost all tags captured in BC are reported (Beamish and McFarlane, 1988); therefore, a W_{BC} of 0.90 is assumed for tag recoveries in BC.

Instantaneous rates of natural mortality M and tag loss H were from values in the literature. An M of 0.10 was obtained from Fujioka (1989). An H of 0.02 was based on a double tagging experiment from Beamish and McFarlane (1988).

Sensitivity Analysis

We conducted a sensitivity analysis on M, W, and $\rho_{BC.EG}$ to evaluate the robustness of parameter estimates. Sensitivity analysis determines the effects of perturbations of input variables on estimated parameters. The relative degree of sensitivity was evaluated by calculating the percent change in the parameter estimates. For the sensitivity analysis, all constants were at their baseline values, as described in the previous section, except for the constant that was examined. The sensitivity to natural mortality and reporting rates was assessed by increasing and decreasing M and W_{NPFMC} by 50%. The sensitivity to $\rho_{BC.EG}$ was assessed by increasing it from 0.0 to 0.05 and 0.10. Estimates of movement parameters are insensitive to assumed values of f because in our formulation f and λ are completely confounded. Thus, a change of input values for f causes a proportional change in λ and no change in estimates of movement parameters. This structural feature of the model was verified by doubling f. As expected, there was a 50% reduction in the estimate of λ and no change in movement parameters.

Results

Baseline Analysis

Parameter estimates were markedly different between the three length groups (Table 1.3). This observation was supported by the likelihood ratio test that indicated a

full model with 12 separate parameters for each length group ($-\log_e L = 4524$) was statistically different ($\chi^2 = 621.8$; $P < 0.001$; 24 df) from a reduced model with 12 parameters in common for each length group ($-\log_e L = 4835$). Estimates of movement parameters $\rho_{i,k}$ ranged from 0.001 to 0.105 for small sablefish, 0.002 to 0.130 for medium sablefish, and 0.001 to 0.454 for large sablefish. For all length groups, the largest estimates were for movement from the Western Gulf of Alaska (WG) to the Central Gulf of Alaska (CG), i.e. ($\rho_{WG,CG}$) and lesser but still sizable movement in the reverse direction ($\rho_{CG,WG}$). The smallest estimates were generally for movement from EG to BC, and the Aleutians (AL) to BS. Estimates of the fishing mortality calibration coefficient λ were similar for medium (1.07) and large (1.12) sablefish but substantially lower for small (0.82) sablefish.

The precision of parameter estimates depended on length at release (Table 1.3). Estimates of movement parameters $\rho_{i,k}$ were generally most precise for medium-length sablefish; values of the coefficient of variation (CV) were usually less than 25%. Estimates of $\rho_{i,k}$ for large sablefish were least precise; CV values were mostly greater than 50%. The higher variability of estimates for large sablefish was reflected in the *t*-statistics, where half of the parameters were not significantly different ($P > 0.05$) from zero even though some point estimates were not near zero. For small and medium-length fish, *t*-statistics were usually not significant only when estimates were near zero. Estimates of λ were very precise for all length groups (CV < 5%) .

Most correlations between parameter estimates were low ($r < 0.6$). Estimated correlation coefficients for medium sablefish are shown in Table 1.4. The magnitude and pattern of correlations for small and large sablefish were similar to those for medium sablefish. Of 66 possible correlations only two were 0.8 or greater: the correlations between $\rho_{CG,EG}$ and $\rho_{EG,CG}$, and between $\rho_{WG,CG}$ and $\rho_{CG,WG}$. Highly correlated estimates indicate that parameters are confounded and difficult to determine uniquely from one

another. These high correlations are not of particular concern because estimates of these parameters had low CV values (Table 1.3).

Table 1.3. Maximum likelihood estimates of monthly instantaneous movement rates from area i to area k ($\rho_{i,k}$), fishing mortality calibration coefficients (λ), coefficients of variation (CV), probability levels for t-tests (P), and log-likelihoods ($\log_e(L)$) for three length groups of tagged sablefish in the northeastern Pacific.

Parameter	Small (<57 cm FL)			Medium (57-66 cm FL)			Large (>66 cm FL)		
	Estimate	CV(%)	P	Estimate	CV(%)	P	Estimate	CV(%)	P
$\rho_{EG,BC}$	0.001	18.22	0.000	0.002	8.32	0.000	0.003	8.54	0.000
$\rho_{EG,CG}$	0.077	22.84	0.000	0.036	11.34	0.000	0.037	22.35	0.000
$\rho_{CG,EG}$	0.040	24.12	0.000	0.045	9.64	0.000	0.096	18.30	0.000
$\rho_{CG,WG}$	0.071	35.42	0.005	0.062	23.43	0.000	0.141	63.95	0.089
$\rho_{WG,CG}$	0.105	39.80	0.011	0.130	21.21	0.000	0.454	69.24	0.111
$\rho_{WG,BS}$	0.029	19.41	0.000	0.018	19.98	0.000	0.019	52.21	0.054
$\rho_{WG,AL}$	0.027	20.69	0.000	0.020	21.38	0.000	0.016	61.71	0.113
$\rho_{BS,WG}$	0.030	19.76	0.000	0.060	11.69	0.000	0.084	29.58	0.001
$\rho_{BS,AL}$	0.002	106.54	0.348	0.004	91.82	0.254	0.031	72.97	0.166
$\rho_{AL,WG}$	0.015	25.90	0.000	0.023	15.73	0.000	0.033	20.13	0.000
$\rho_{AL,BS}$	0.004	46.32	0.031	0.003	50.62	0.050	0.001	213.18	0.644
λ	0.818	3.54	0.000	1.118	2.53	0.000	1.069	4.01	0.000
$\log_e(L)$	-1391.6			-1939.0			-1193.2		

BC, British Columbia; EG, Eastern Gulf of Alaska; CG, Central Gulf of Alaska; WG, Western Gulf of Alaska; BS, Eastern Bering Sea; AL, Aleutians.

Deviations from our model did not exhibit any extreme trends by recovery area (Figure 1.2). For all the size groups, deviances for AL and BC were slightly more prevalent when observed tag recoveries were greater than predicted. The overall deviance summed over size groups ($\sum deviance$ = 5393.88) was statistically significant (χ^2= 4239.63; P< 0.001; 3942 df) indicating there may be evidence the observed tag recoveries differed significantly from that expected by the model. However, the use of the overall deviance as a goodness-of-fit statistic is open to objections, and a large overall deviance cannot necessarily be considered as evidence of a poor fit (McCullagh and Nelder, 1983).

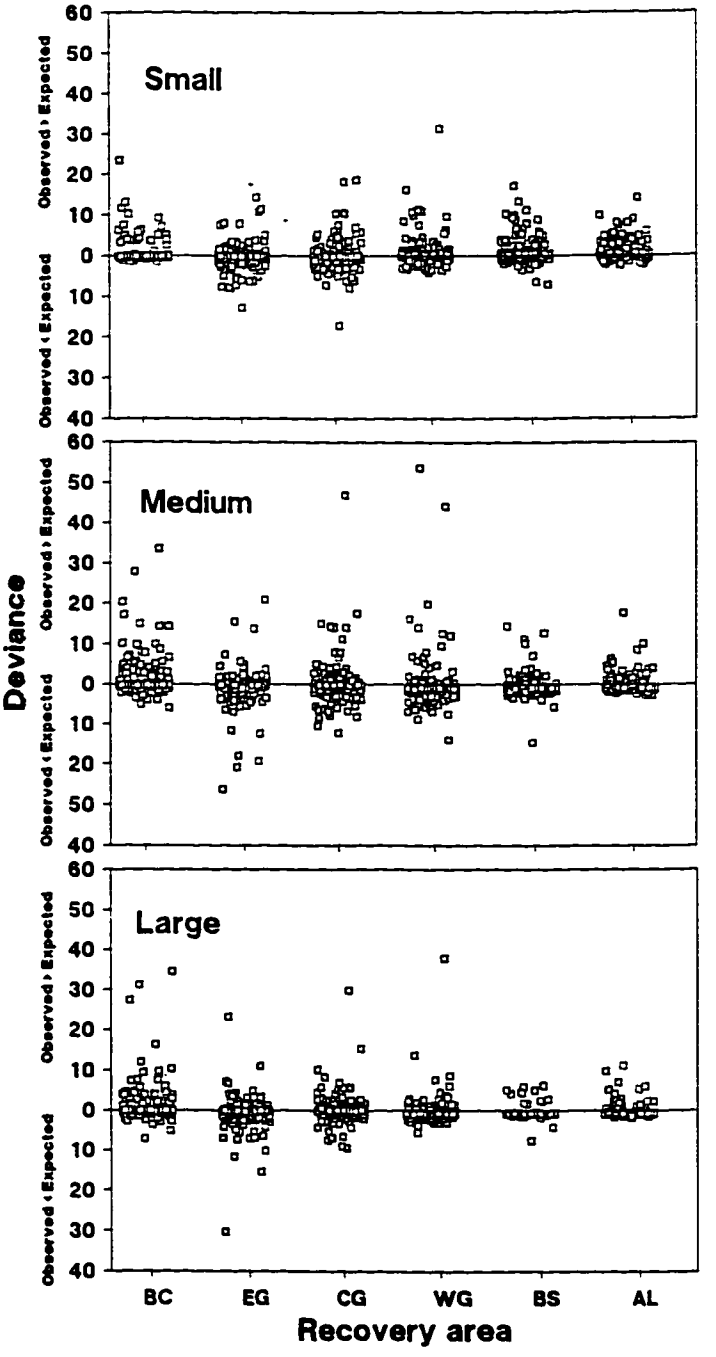

Figure 1.2. Deviances by recovery area for small (less than 57 cm FL), medium (57-66 cm FL), and large (more than 66 cm FL) tagged sablefish in the northeast Pacific. There are 221 observations for each recovery area-length group category.

The large amount of movement among areas was most evident when the $\rho_{i,k}$ values were converted to annual rates (Table 1.5). Estimated annual movement rates out of an area ranged from 19 to 69% for small, 25 to 72% for medium, and 27 to 71 % for large sablefish. The annual percentage leaving WG was the greatest for small and medium sablefish, whereas the percentage leaving the Eastern Bering Sea (BS) was greatest for large sablefish.

Table 1.4. Parameter correlations for medium-length sablefish estimated by the inverse Hessian method.

	$\rho_{EG,BC}$	$\rho_{EG,CG}$	$\rho_{CG,EG}$	$\rho_{CG,WG}$	$\rho_{WG,CG}$	$\rho_{WG,BS}$	$\rho_{WG,AL}$	$\rho_{BS,WG}$	$\rho_{BS,AL}$	$\rho_{AL,WG}$	$\rho_{AL,BS}$
$\rho_{EG,CG}$	0.116										
$\rho_{CG,EG}$	0.009	0.799									
$\rho_{CG,WG}$	-0.019	-0.291	-0.159								
$\rho_{WG,CG}$	-0.016	-0.312	-0.258	0.926							
$\rho_{WG,BS}$	-0.004	0.006	-0.026	-0.256	-0.153						
$\rho_{WG,AL}$	-0.009	0.033	-0.012	-0.191	-0.098	-0.120					
$\rho_{BS,WG}$	-0.005	0.054	0.009	-0.409	-0.406	0.546	0.302				
$\rho_{BS,AL}$	-0.004	-0.054	-0.025	0.268	0.256	-0.052	-0.536	-0.460			
$\rho_{AL,WG}$	0.001	0.042	0.021	-0.263	-0.246	0.164	0.543	0.176	-0.194		
$\rho_{AL,BS}$	0.002	-0.023	-0.014	0.116	0.104	-0.273	-0.026	-0.062	0.113	-0.267	
λ	-0.144	0.070	-0.007	0.019	0.009	-0.019	0.057	0.013	0.020	-0.026	-0.011

BC, British Columbia; EG, Eastern Gulf of Alaska; CG, Central Gulf of Alaska; WG, Western Gulf of Alaska; BS, Eastern Bering Sea; AL, Aleutians.

The pattern of movement depended on length at release (Table 1.5). Large sablefish in the middle NPFMC areas (CG and WG) had a greater tendency to move eastward compared with small sablefish, although some estimates for large sablefish were highly variable. Medium sablefish had a slight inclination for eastward movement. For example, annually more than 46% of the large sablefish in CG moved eastward to EG, whereas about 10% moved westward in the opposite direction towards WG, BS, and AL. Small sablefish in CG had the reverse pattern, with 19% moving eastward and 32%

westward. Thus, the direction of movement along the continental slope was mostly eastward (clockwise) for large sablefish and westward (counter-clockwise) for small sablefish.

The pattern of movement also depended on length at release in the peripheral NPFMC areas (EG, BS, and AL; Table 1.5). Large and medium sablefish had a greater tendency to remain in EG than small sablefish; annually, 27% of the large and 30% of the medium sablefish moved from EG, whereas 51% of the small sablefish moved from EG. The pattern was reversed in BS and AL, where small sablefish had a greater tendency to remain than medium and large sablefish. Yearly, 29% and 19% of the small sablefish moved from BS and AL, respectively, whereas 51% and 25% of the medium and 73% and 33% of the large sablefish moved from BS and AL, respectively.

Sensitivity Analysis

Most movement parameters were robust to perturbations of input constants. The results of sensitivity analysis for medium sablefish are shown in Figure 1.3. Results for small and large sablefish were similar to those for medium sablefish. Compared with a 50% increase in an input constant, a 50% decrease usually resulted in a change in a parameter that had the opposite direction but not necessarily the same magnitude. This difference in magnitude can be attributed to the non-linearity of the model structure. A 50% change in natural mortality M caused less than an 11% change in the magnitude of $\rho_{i,k}$ values. A 50% change in reporting rates W(NPFMC) caused less than a 10% change in the magnitude of $\rho_{i,k}$ values, except for $\rho_{EG,BC}$ which changed about 45%. The $\rho_{EG,BC}$ parameter was extremely sensitive to changes in the ρ(BC,EG) input constant. Increasing ρ(BC,EG) to 0.05 and 0.10 caused a 112% and 224% increase in $\rho_{EG,BC}$, respectively, but less than a 10% change in the magnitude of the other movement parameters.

The fishing mortality calibration parameter λ was highly sensitive to perturbations of W_{NPFMC}, but robust to perturbations in M and $\rho_{BC,EG}$ (Figure 1.3). Compared with a

50% increase in W_{NPFMC}, a 50% decrease caused a substantially larger change in λ (122% vs. -36%) .

Table 1.5. Estimated annual movement probabilities ($\theta_{i,k}$) converted to percentages for three length groups of tagged sablefish. Each estimate is followed by its standard error. Total ($i \neq k$) is the estimated annual movement out of area i.

From area i	To area k						
	BC	EG	CG	WG	BS	AL	Total ($i \neq k$)
Small (<57 cm FL)							
EG	0.829	48.522	37.518	10.746	1.209	1.176	51.478
	0.148	6.166	5.872	2.414	0.315	0.332	6.166
CG	0.145	19.409	48.371	22.852	4.639	4.584	51.629
	0.038	3.259	4.140	4.387	1.073	1.193	4.140
WG	0.036	7.817	32.137	30.796	14.502	14.712	69.204
	0.013	2.091	7.392	5.175	3.022	3.283	5.175
BS	0.003	0.980	7.260	16.053	71.013	4.116	28.987
	0.001	0.287	1.919	3.465	3.508	2.028	3.508
AL	0.001	0.528	4.012	9.260	4.935	81.263	18.737
	0.001	0.185	1.281	2.388	1.411	3.045	3.045
Medium (57-66 cm FL)							
EG	1.708	69.928	22.320	5.303	0.339	0.404	30.072
	0.144	2.306	2.142	0.800	0.075	0.095	2.306
CG	0.318	27.211	47.396	19.801	2.338	2.936	52.604
	0.038	2.030	2.161	2.229	0.473	0.618	2.161
WG	0.101	13.349	40.866	28.479	7.242	9.962	71.521
	0.016	1.521	3.082	2.765	1.388	1.970	2.765
BS	0.014	2.917	16.482	24.614	49.360	6.612	50.640
	0.002	0.369	1.804	2.990	3.038	2.180	3.038
AL	0.006	1.294	7.748	12.767	3.383	74.802	25.198
	0.001	0.230	1.243	1.851	0.990	2.791	2.791
Large (>66 cm FL)							
EG	2.602	73.128	19.473	4.268	0.241	0.288	26.872
	0.230	0.388	5.943	6.057	0.309	0.269	3.388
CG	0.850	46.798	42.271	7.303	1.096	1.683	57.729
	0.168	13.685	49.519	58.010	3.187	1.956	49.519
WG	0.414	26.105	11.510	51.459	4.617	5.895	48.541
	0.403	60.464	254.060	295.025	16.626	6.892	295.025
BS	0.086	9.531	18.107	25.890	28.628	17.759	71.372
	0.071	11.978	52.093	59.814	9.804	9.822	9.804
AL	0.039	4.665	10.305	15.525	1.818	67.649	32.351
	0.030	5.052	21.834	25.500	2.022	4.803	4.803

BC, British Columbia; EG, Eastern Gulf of Alaska; CG, Central Gulf of Alaska; WG, Western Gulf of Alaska; BS, Eastern Bering Sea; AL, Aleutians.

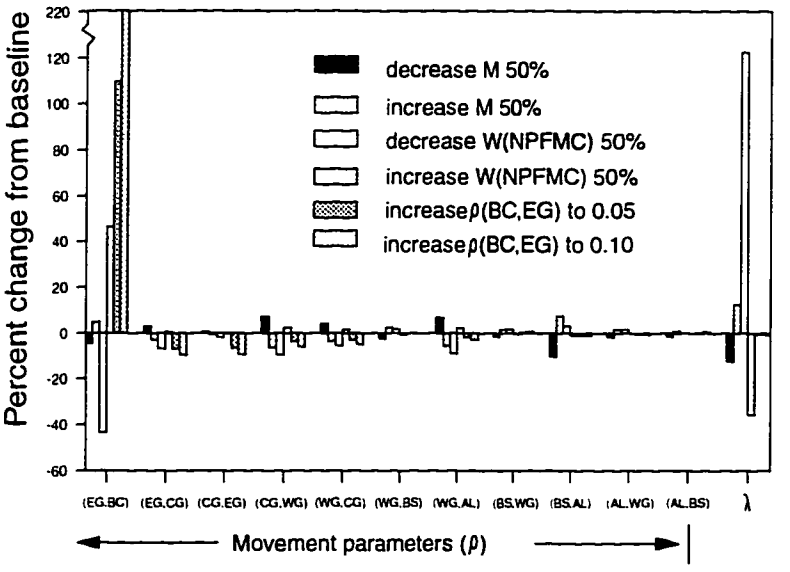

Figure 1.3. Sensitivity of parameter estimates for medium-length sablefish to perturbations of input constants.

Discussion

The goal of this analysis was to quantify annual movement rates of sablefish among fishery regulatory areas. Application of Hilborn's (1990) method to sablefish tag data proved a flexible tool for estimating movement rates and their standard errors. Earlier studies relied mostly on more qualitative methods (Bracken, 1982; Dark, 1983; Fujioka *et al.*, 1988). Beamish and McFarlane (1988) presented a detailed analysis of Canadian tag data, but they did not explicitly estimate movement rates or evaluate error.

The use of a Markov model to describe the dynamics of sablefish movement was based on a compromise between limitations of available data and biological realism (also see Deriso *et al.*, 1991). All fish at a particular place and time are assumed to have the same movement probabilities independent of where they were at previous times. An alternate hypothesis of fish movement is a process where movement probabilities for each fish may depend on previous movements or genetic/physiological cues. Fitting such a model probably requires data in the form of multiple recaptures of tagged fish. Such data

do not exist for sablefish because tag returns were almost exclusively from the commercial fishery where tagged fish are not released after being captured.

Given sufficient data, the model specified here provided precise and unconfounded estimates for most parameters. Only for large sablefish were some estimates unsatisfactory. Movement of large sablefish is less adequately described by the model than the other length groups, or the number of releases and subsequent recoveries were insufficient. Although a third to half of the exploitable population in the study area were large sablefish (Clausen and Sigler, 1991), only 17% of the fish tagged were large. We recommend that more large sablefish should be tagged in future studies.

Estimates of movement attained here are based on the assumption that movement rates are constant over time. A rapid increase in the abundance of sablefish has occurred in the study area during the time period of this study (Sigler and Fujioka, 1988). Movement rates may, therefore, not be indicative of previous or future periods.

Given the results of sensitivity analysis, estimates of movement parameters appear to be fairly robust. Only one estimated movement parameter ($\rho_{EG,BC}$) was highly sensitive to perturbations of input constants. Thus, the reliability of the estimates of movement rates from EG to BC obtained here is questionable. Inclusion of results from tagging studies in British Columbia (Beamish and McFarlane, 1988) may allow reliable estimation of this parameter.

Our sensitivity analysis did not appraise all possible sources of uncertainty in the model structure or input constants. Such a definitive analysis was not within the scope of this study. Area-specific biases in input constants could influence estimates of movement considerably. The slightly uneven distribution of model deviations by area indicates that the calibration parameter λ and reporting rates W may have some area specificity. Input values for fishing mortality and reporting rates used here relied heavily on reported catches and biomass estimates, which are subject to inherent bias and measurement error

(McDevitt, 1986; Fujioka, 1989). Consideration of such factors in a comprehensive sensitivity analysis should be the focus of future analyses.

The estimate of λ was lowest for small sablefish. This result indicates that there is size-specific selectivity of the commercial fishing gear, probably because the distribution of sablefish of less than 57 cm FL encompasses depths shallower than the commercial fishery (Sasaki, 1985). Given the uncertainty of fishing mortality input constants f, we were surprised at the closeness of estimates of λ for medium and large sablefish to one. This implies that our input values for f were reasonable estimates of fishing mortality. Considerable uncertainty still exists because λ was sensitive to input constants, especially reporting rates.

The magnitude and pattern of movement rates among NPFMC areas indicates that movement influences the amount of fish available for harvest in an area. If the passage of fish through an area is large relative to fishing mortality, localized fishing probably has little impact on short-term abundance in an area. The results indicated that harvest rates throughout the study area were usually less than 10%, considerably less than the amount of movement. This large amount of movement is in contrast to British Columbia waters where most tagged adult sablefish remained in the release area (Beamish and McFarlane, 1988).

We concur with Sasaki (1985) that high annual movement rates among NPFMC areas may negate strict management by regulatory area, yet little is known about the location of spawning areas of sablefish or whether specific spawning grounds exist. Most recruitment of sablefish in the NPFMC area has been hypothesized to originate from fish that spawn in British Columbia and the eastern parts of the Gulf of Alaska (Bracken, 1982; Beamish and McFarlane, 1988). Additionally, populations in the eastern Bering Sea and Aleutians are believed to be maintained by emigrants from other areas (Sasaki, 1985; Beamish and McFarlane, 1988). Our results confirm that small, mostly immature, sablefish predominantly move towards the Bering Sea and Aleutians, and large mature

sablefish move in the opposite direction. Thus, a management strategy may be needed to ensure that spawning aggregations are not overfished.

Incorporation of movement rates obtained here into a yield analysis may help explain observed temporal changes in abundance and size distribution in each area (Clausen and Sigler, 1991). An analysis based on length or age structure that includes movement is a logical next step. A promising approach is the recent method of catch-age analysis for migratory populations (Quinn *et al.*, 1990). Given catch-age data, some auxiliary information, and movement rates, this method provides area-specific estimates of population parameters such as year-class strength and exploitable biomass. Such an analysis will help determine the interactions among fisheries in different areas and may ultimately lead to improved management of this important resource.

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Chapter 2.

Geographic Apportionment of Sablefish Harvest in the Northeastern Pacific Ocean[2]

Abstract

An age-structured model of the sablefish population in the northeastern Pacific Ocean that includes movement, survival, and recruitment was constructed to examine yield-per-recruit and harvest policies. The model includes a Markov transition matrix that specifies the probability that a fish of a given age will move from one fishery regulatory area to another in one year. Estimates of yield-per-recruit are sensitive to assumptions about the geographic distribution of recruitment. If most recruitment originates in the eastern areas of the Gulf of Alaska, then fisheries in the western regions will benefit from low exploitation rates. Conversely, if recruitment originates in all geographic areas, then fisheries in the eastern area will benefit from low exploitation rates. In general, when evaluated under the current annual exploitation rate of about 10% over a 100-year period, policies that apportion harvest among regulatory areas based on areal estimates of available biomass or based on the steady-state distribution of biomass computed from the transition matrices gave similar results. The current policy of apportionment is based on a weighted moving average of areal estimates of available biomass. This policy adapts to current information about geographic distribution of biomass, reduces the effects of annual fluctuations in biomass estimates due to measurement error, and does not require estimates of movement probabilities for implementation.

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[2]An earlier version of this chapter is Heifetz, J., Fujioka, J.T., and Quinn, T.J. II. 1996. Geographic apportionment of sablefish harvest in the northeastern Pacific Ocean. *In* International Symposium on the Biology and Management of Sablefish. NOAA Technical Report NMFS (in press).

Introduction

The apportionment of catch limits among geographic areas for many groundfish fisheries is based on the geographic distribution of estimated abundance. Surprisingly, few studies have compared alternative methods of apportioning catch limits, partly because of lack of information on the spatial aspects of many fish populations. The purpose of this paper is to explore alternative methods of apportioning the annual catch limits for a highly migratory species: sablefish (*Anoplopoma fimbria*) in the northeastern Pacific Ocean.

Plans are underway to manage the United States fishery for sablefish in the northeastern Pacific Ocean by individual transferable fishing quotas (IFQs) on an areal basis. Under this management system, an individual will own the right to a certain portion of the catch limit within an area. Thus, apportioning the catch limit among areas can have important social and economic effects.

Annual catch limits for sablefish in waters managed by the North Pacific Fishery Management Council (NPFMC) are typically apportioned among fishery regulatory areas in direct proportion to geographic distribution of estimated biomass (Gulf of Alaska Groundfish Plan Team, 1992). Tagging experiments indicate rapid mixing of sablefish among regulatory areas; the pattern of movement is related to fish size and age (Heifetz and Fujioka, 1991). Movement is primarily westward for small, mostly immature sablefish and eastward for large, mature sablefish. Large sablefish in the Eastern Gulf of Alaska regulatory area (EG) tend to remain there. This pattern of movement has not been directly considered in the development of harvest strategies in the past.

In this paper, we use movement rates estimated from tagging data reported by Heifetz and Fujioka (1991[chapter 1]), and other sablefish population parameters to model the movement, survival, growth, and recruitment of an age-structured population. Including movement rates in a population model is an important step towards understanding the spatial dynamics of an exploited population.

Our study is divided into two parts, each with different objectives. First, yield-per-recruit by area is analyzed to explore the implications of movement and assumptions about the geographic distribution of recruitment with regard to sablefish population dynamics. Second, alternative strategies for geographic distribution of harvest are evaluated. Trends in yield, yield variability, reproductive potential, and catch per unit effort are examined.

Methods

Model Description

In our population dynamics model, we attempt to accommodate the dynamics of the survival, movement, and recruitment processes and the methods used by the NPFMC for setting sablefish catch limits in the northeastern Pacific Ocean (Figure 2.1). Typically, a biomass-based Acceptable Biological Catch (ABC) for all regulatory areas combined is computed by multiplying available biomass B for all areas combined by an exploitation rate μ. This ABC is then apportioned to the five regulatory areas based on some policy. We equate ABC with a catch limit and assume that the entire catch limit is taken each year. Because sablefish in the northeastern Pacific Ocean is a fully utilized species and managed on a quota system, this assumption is approximately correct. Given numbers $N_{a,t,i}$ at age a in area i at the beginning of year t, weight at age w_a, availability at age s_a, and apportionment $P_{t,i}$ (proportion of catch limit allotted to area i in year t), available biomass is

$$B_{a,t,i} = N_{a,t,i} w_a s_a .$$

The total catch limit among areas is

$$Q_t = \mu B_t ,$$

which is apportioned to areas as

$$Q_{t,i} = Q_t P_{t,i} \ .$$

Exploitation rate by area is

$$\mu_{t,i} = \frac{Q_{t,i}}{\sum_a B_{a,t,i}} .$$

Catch in numbers at age is then obtained as

$$C_{a,t,i} = \mu_{i,t} N_{a,t,i} s_a \ .$$

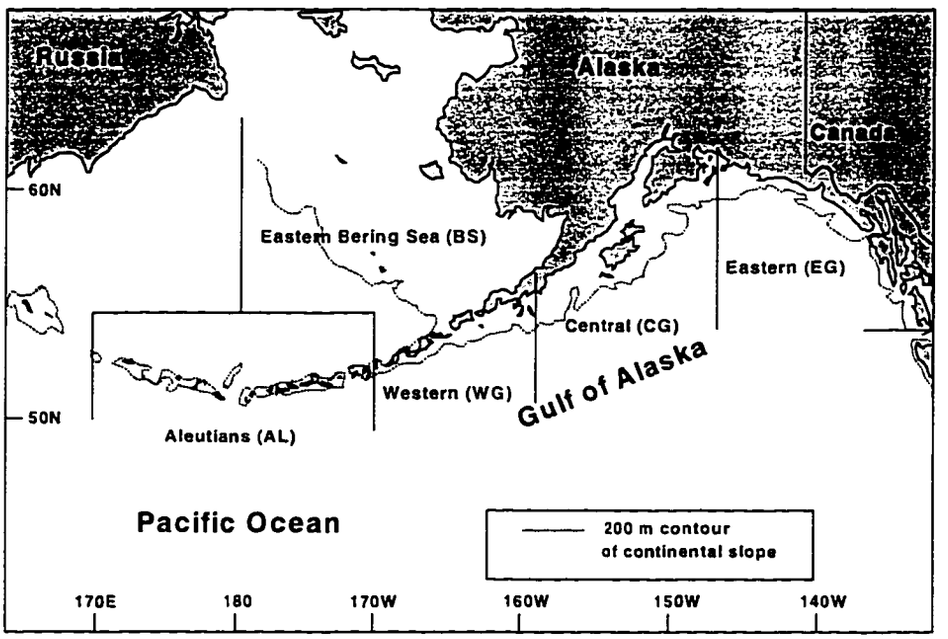

Figure 2.1. Northeast Pacific Ocean showing North Pacific Fishery Management Council (NPFMC) regulatory areas. Abbreviations for areas that are used throughout the text are in parentheses.

For convenience, natural mortality M is assumed to occur continuously throughout the year and fishing to occur instantaneously at the beginning of a year. Abundance in each area after fishing and natural mortality is

$$N^{*}_{a,t,i} = (N_{a,t,i} - C_{a,t,i})\exp(-M).$$

Movement is assumed to occur instantaneously at the end of a year. Given the Markov matrix of annual movement rates Θ_a where the i,k^{th} element of Θ_a is the proportion of age-a fish from area i that move to area k in a year, the row vector of numbers at age a+1 at the beginning of year t+1 after movement is

$$N_{a+1,t+1} = N^{*}_{a,t}\,\Theta_a \,. \qquad (2.1)$$

Quinn *et al.* (1990a) describe a similar population dynamics model with movement. The order of events in our formulation is different from theirs. We have movement occur at the end of a year, whereas they have movement occur at the beginning of a year. The order of events is somewhat arbitrary and alternative orders should not produce substantially different results (Getz and Haight, 1989).

Table 2.1 summarizes population parameters for natural mortality, weight, availability, maturity, and growth for sablefish in the northeastern Pacific Ocean. Although male and female sablefish have different growth patterns, we use growth parameters for both sexes combined because movement rates are estimated for both sexes combined. Movement rates given in Heifetz and Fujioka (1991 [chapter 1]) are based on fish length. We convert these length-specific movement rates to age-specific movement rates using von Bertalanffy growth parameters (Table 2.2).

Table 2.1. Estimates of population parameters for sablefish in the northeastern Pacific Ocean. Fraction mature and availability at age are from Sigler and Fujioka (1993). Growth parameters are adapted from Lowe et al. (1991).

Age a	3	4	5	6	7	8	9	10	11	12	13-75
Natural mortality M	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10
Maturity m_a	0.002	0.032	0.232	0.629	0.868	0.949	0.977	0.988	0.993	0.998	1.00
Availability s_a	0.15	0.32	0.48	0.63	0.73	0.82	0.88	0.93	0.97	1.00	1.00
von Bertalanffy model	Allometric weight-length model										
L_a(cm)=L_∞(1-exp(-k(a-t_0)))	w_a(kg)=cL_a^b										
L_∞ = 80.550	c = 2.72 X 10^{-6}										
k = 0.171	b = 3.325										
t_0 = -3.220											

Geographical Yield-per-recruit

First, we investigate the effects on yield-per-recruit of different geographic distributions of recruitment. In yield-per-recruit analyses, the effects of fishing are surmised by following a cohort through time during its fishable life span. In our analysis, the relative recruitment may differ by area. Given that recruitment starts at age 3, the abundance of a cohort at age 3 is

$$N_{3,t,i} = R_i \ .$$

Yield-per-recruit Y_i/R is calculated for each area separately over a range of $0.0 \le \mu \le 0.7$. For each μ, the population dynamics model simulates a 75-year period then yield-per-recruit is calculated from

$$\frac{Y_i}{R} = \frac{\mu \sum_a s_a N_{a,i} w_a}{R},$$

Table 2.2. Annual movement rates from one area to another for different age groups of sablefish; adapted from Heifetz and Fujioka (1991 [chapter 1]).

From area (i)	To area (k)				
	EG	CG	WG	BS	AL
Age 3-4					
EG	0.489	0.378	0.109	0.012	0.012
CG	0.194	0.484	0.229	0.047	0.046
WG	0.078	0.322	0.308	0.145	0.147
BS	0.010	0.073	0.160	0.710	0.047
AL	0.005	0.040	0.093	0.049	0.813
Age 5-8					
EG	0.712	0.227	0.054	0.003	0.004
CG	0.273	0.476	0.199	0.023	0.029
WG	0.134	0.409	0.285	0.072	0.100
BS	0.029	0.165	0.246	0.494	0.066
AL	0.013	0.077	0.128	0.034	0.748
Age $ 9					
EG	0.751	0.200	0.044	0.002	0.003
CG	0.472	0.426	0.074	0.011	0.017
WG	0.262	0.116	0.517	0.046	0.059
BS	0.095	0.181	0.259	0.287	0.178
AL	0.047	0.103	0.155	0.018	0.677

EG, Eastern Gulf of Alaska; CG, Central Gulf of Alaska; WG, Western Gulf of Alaska; BS, Eastern Bering Sea; AL, Aleutians.

where R is recruitment for all areas combined. Because R is a constant on both sides of the above equation, it can be eliminated to compute Y_i. Apportionment among areas is set in proportion to available biomass in each area. Thus, exploitation rate among areas was constant (i.e., $\mu = \mu_{t,i}$).

We construct three alternative hypotheses concerning the geographic distribution of annual recruitment to examine effects on areal yields (Table 2.3). Hypothesis A: recruitment occurs equally in all areas. Hypothesis B: most recruitment occurs in the EG with a progressively lower proportion in the more westward areas. Hypothesis C: all recruitment occurs in the EG.

Table 2.3. Three hypotheses for the geographic distribution of annual recruitment of sablefish.

	Area				
Hypothesis	EG	CG	WG	BS	AL
A	0.20	0.20	0.20	0.20	0.20
B	0.40	0.30	0.20	0.05	0.05
C	1.00	0.00	0.00	0.00	0.00

EG, Eastern Gulf of Alaska; CG, Central Gulf of Alaska; WG, Western Gulf of Alaska; BS, Eastern Bering Sea; AL, Aleutians.

These hypotheses represent a range that we believe reasonably approximates the uncertainties about geographic distribution of recruitment. Considered in development of these hypotheses is the pattern of sablefish movement (Heifetz and Fujioka, 1991 [chapter 1]). The westward movement of immature sablefish may compensate for the centering of recruitment in the eastern areas. Thus, two of the three hypotheses have the highest proportion of recruitment in the EG. Estimation of the geographical distribution of recruitment and assignment of probabilities to alternative hypotheses may be possible from survey data. This is not within the scope of our study.

Alternative Apportionment Policies

In this part of the study, we modify the yield-per-recruit analysis to add biological realism and measurement error. Stochasticity is incorporated by making recruitment based on past observations (Sigler and Fujioka, 1993). Each year a recruitment level is randomly chosen from the 12 past observations (Figure 2.2).

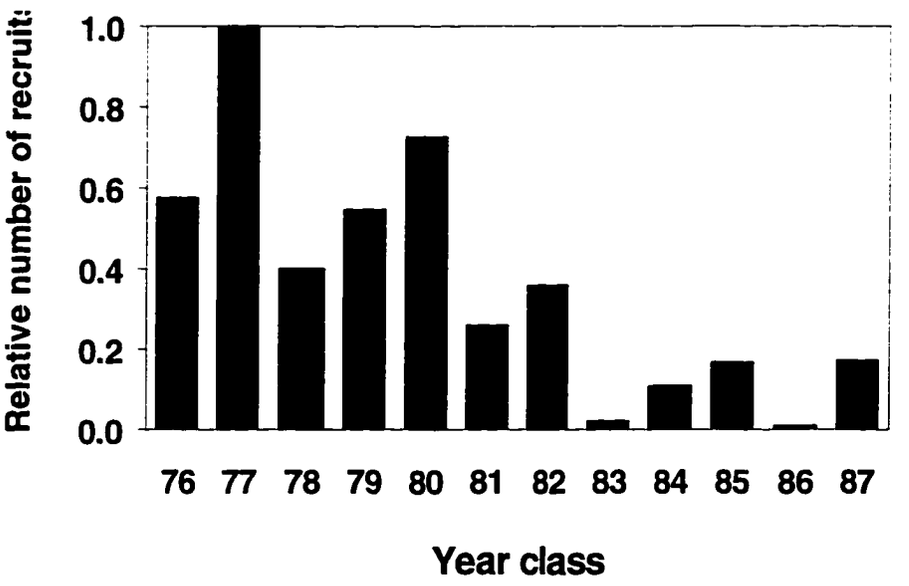

Figure 2.2. Estimated relative number of sablefish recruits, 1976-1987 (Sigler and Fujioka, 1993).

This method does not assume any functional form to the stock and recruitment relationship, but instead assumes there is no relationship between stock size and resulting recruitment and that recruitment levels observed in the past are equally likely to occur in the future. Recruitment is distributed among the areas according to the three hypotheses of the yield-per-recruit analysis.

Description of Policies

Four alternative policies of apportionment of sablefish catch quotas among areas are evaluated:

Policy 1--Constant apportionment among areas. Because there are five areas, all $P_{t,i} = 0.20$.

Policy 2--Set the areal catch limits proportional to estimated available biomass in each area. Given estimated available biomass $\hat{B}_{t,i}$ summed over all ages in an area, apportionment is

$$P_{t,i} = \frac{\hat{B}_{t,i}}{\sum_i \hat{B}_{t,i}} .$$

where

$$\hat{B}_{t,i} = B_{t,i} + \epsilon_t .$$

Variable ϵ_t is a normally distributed random error term with mean 0 and constant coefficient of variation (cv) [i.e. variance = $(B^2_{t,i}cv^2)$]. This error term represents the measurement error associated with the estimation of available biomass. The cv is estimated to be 0.10 based on analysis of areal variability observed in the annual longline survey of sablefish in the Gulf of Alaska (M. Sigler, Auke Bay Lab., Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 11305 Glacier Highway, Juneau AK 99801-8626, personal communication, March 1993).

Policy 3--Set the catch limits proportional to a weighted moving average of apportionment given in policy 2. The most recent year is given a weight of two and the prior four years are given a weight of one. This is the present method of apportionment (Gulf of Alaska Groundfish Plan Team, 1992).

Policy 4--Apportion areal catch limits on the basis of the estimated steady-state distribution of available biomass. Given equation (2.1), a steady state distribution of available biomass exists for each level of exploitation and recruitment hypothesis. As long as the θ_a's do not change, the distribution of available biomass will approach a limit. The expected value of the steady-state distribution is determined by simulation. The population dynamics model is simulated for 200 years with stochastic recruitment. This simulation is replicated 200 times, each with a different random sequence of recruitment. The apportionments for this policy are based on the mean of the 200 replications of the geographic distribution of available biomass at the end of the 200-year period. Exploitation rate among areas is constant (i.e., $\mu = \mu_{t,i}$). Table 2.4 shows the apportionments based on this policy. Stochastic recruitment causes variability in the estimates of the steady-state distribution of available biomass.

Performance Criteria

Two hundred replications over 100 years are performed for each combination of the four apportionment policies and three recruitment hypotheses. A particular combination of a policy and recruitment hypothesis (a scenario) is analyzed, giving 12 scenarios. A common random-number sequence is used for each scenario. Exploitation rate μ is set at 0.10, which approximates the current level of exploitation (Fujioka, 1992; Lowe, 1992). An example of the apportionments resulting from a typical replication for recruitment hypothesis B is shown in Figure 2.3.

Table 2.4. Apportionment of sablefish harvest among areas for three hypotheses of the geographic distribution of annual recruitment based on the mean steady-state distribution of available biomass for 200 replicates. Exploitation rate equals 0.10. The coefficient of variation is in parentheses.

	Area				
Hypothesis	EG	CG	WG	BS	AL
A	0.41 (0.07)	0.26 (0.02)	0.15 (0.03)	0.05 (0.19)	0.13 (0.08)
B	0.45 (0.05)	0.28 (0.04)	0.15 (0.03)	0.04 (0.13)	0.09 (0.04)
C	0.52 (0.03)	0.27 (0.04)	0.13 (0.02)	0.02 (0.07)	0.06 (0.07)

EG, Eastern Gulf of Alaska; CG, Central Gulf of Alaska; WG, Western Gulf of Alaska; BS, Eastern Bering Sea; AL, Aleutians.

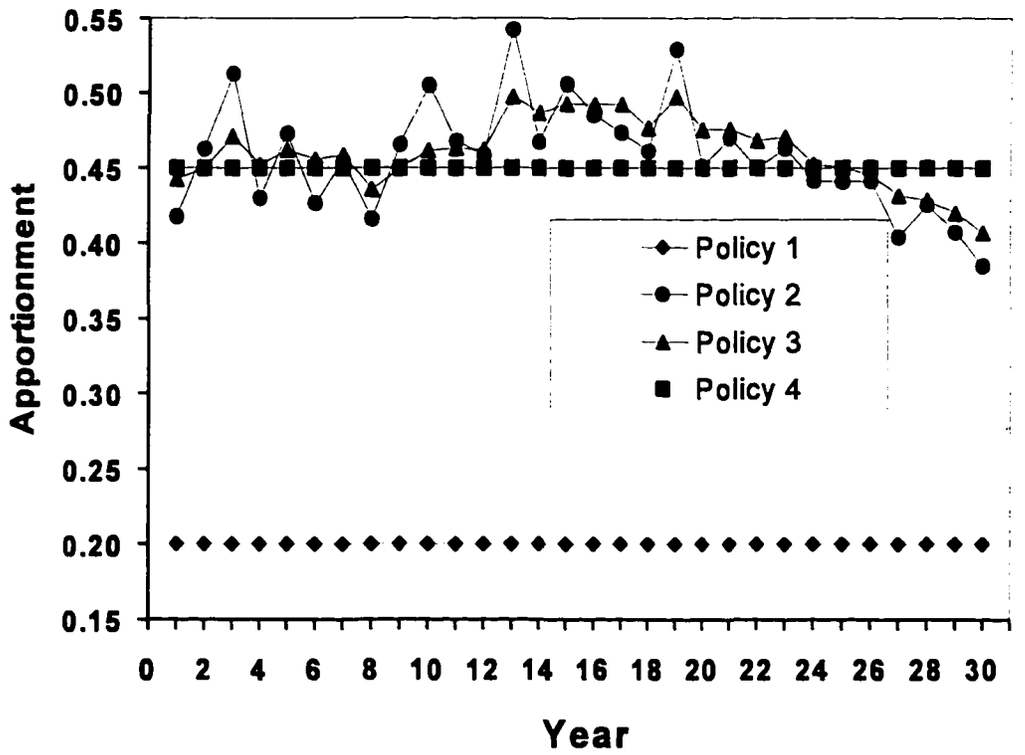

Figure 2.3. A representative time series of catch limit apportionments for the Eastern Gulf of Alaska that would result from the four policy options under hypothesis B.

To evaluate the effects of different apportionment policies, we compare attributes among policies. These attributes include average annual yield, yield variability (*cv*), risk, and catch per unit effort (CPUE). Average annual yield is the mean of the 200 replications. Yield variability is the mean of the 200 replications for the *cv* of the annual yield. Risk is arbitrarily defined as the proportion of the time spawning biomass in an area was less than 30% of the unfished level. This 30% level corresponds to the definition of overfishing used by the NPFMC. Spawning biomass in an area is

$$SB_{t,i}=\sum_{a} N_{a,t,i} m_i w_i \ .$$

The unfished level of spawning biomass is found by letting μ=0. It may be contended that the definition of risk chosen is unfounded because we have assumed that recruitment is independent of spawning biomass. We believe this risk is still a useful attribute for policy comparisons, because there is considerable uncertainty about the relationship between stock and recruitment for sablefish. Attributes are presented for each regulatory area and for all regulatory areas combined.

We assume CPUE is proportional to the density of fish in an area, where density is defined as an area's available biomass divided by its available habitat for sablefish. Available habitat is defined as the combined area of gullies deeper than 400 m and the continental shelf deeper than 200 m (Fujioka, 1992).

Results

Geographical Yield-per-recruit

Results of the geographic yield-per-recruit analysis are sensitive to assumptions about the geographic distribution of recruitment (Figure 2.4). For hypothesis A (where all areas have equal recruitment), the exploitation rate that results in maximum yield-per-

recruit (μ_{max}) is much lower for EG than for the other areas. As exploitation rate increases, a higher proportion of sablefish are caught in the more westward areas before they can return to the EG. Thus, the highest yield for the EG is obtained under low fishing rates where fish are allowed to grow, mature, and move to the EG. For hypothesis B (where most recruitment originates in the Western Gulf of Alaska regulatory area [WG], Central Gulf of Alaska regulatory area [CG], and the EG) the same trend is evident. For hypothesis C (where all recruitment originates in EG), μ_{max} is much lower for the Aleutians (AL) and to some extent the Eastern Bering Sea (BS) and WG than for the more eastward areas. Under this hypothesis, the westward areas depend on migrants from the EG because no recruitment occurs in the westward areas. With a low μ, fish that recruit to the eastward areas can move westward before they are caught.

Alternative Apportionment Policies

Results differ among the regulatory areas, but the three recruitment hypotheses provide similar results for most attributes (Table 2.5). Thus, results apply to the average of the three recruitment hypotheses.

For the easternmost regulatory areas (EG and CG), average annual yields are lowest for policy 1 (equal apportionment) and similar for the other three policies. In the EG, yield for policy 1 is only 43% of the yields for the other policies, and in the CG, yield for policy 1 is only 74% of the yields for the other policies. The pattern is reversed in the more westward areas (WG, BS, AL), where policy 1 has the greatest yield. For these westward areas, yields for policies 2-4 were only about 20-70% of the yield obtained for

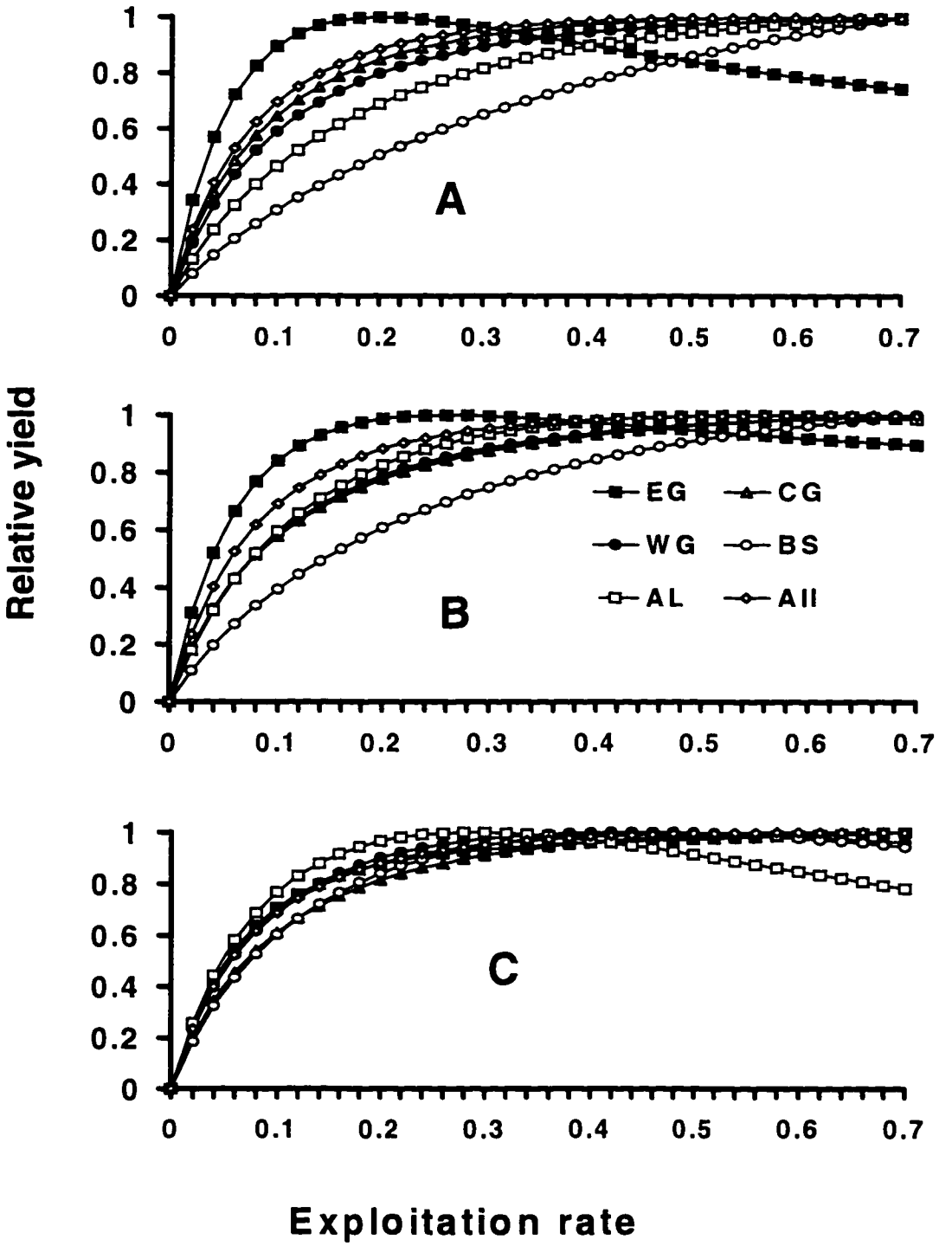

Figure 2.4. Yield relative to the maximum within an area for three hypotheses (A-C) about the geographic distribution of sablefish recruitment.

policy 1. For all areas combined yields are lowest for policy 1 and similar among the other policies.

Regardless of area, yield tends to vary most for policy 2. For the EG and CG, yield varies least for policy 3, whereas for the CG yield varies least for policy 4. For the more westward areas, yield varies least for policy 4. For all areas combined, yield varies least for policy 1 and most for policy 2.

In the EG, CPUE is greatest for policy 1 and similar for the other policies. In the more westward areas, CPUE for policies 2-4 is similar, but is lower for policy 1. For these westward areas, CPUE for policy 1 is 65-80% of the maximum CPUE within an area. For all areas combined, CPUE is similar for policies 2-4 and substantially lower for policy 1.

In the EG, the risk of overfishing (the proportion of the time spawning biomass is below 30% of the unexploited level) is lowest for policy 1 and similar among the other policies. In the CG, all policies had the same level of risk. In the WG, BS, and AL risk is greatest when associated with policy 1. For policy 1 in these westward areas, spawning biomass is below 30% of the unexploited level 13-48% of the time compared to only 3-6% of the time for the other policies. For all areas combined, risk is slightly greater for policy 1 and identical among the other policies.

Discussion

Our goal was to incorporate movement patterns of sablefish into a yield-per-recruit analysis, evaluate alternative apportionment policies, and examine the sensitivity of results to different hypotheses about geographic distribution of recruitment. Including movement rates in an age-structured model of sablefish has increased our understanding of how the fisheries for sablefish in different areas may interact with each other.

The yield-per-recruit in an area is a function of exploitation rates, movement rates, and the distribution of recruitment. If the populations in the westward areas are mostly

Table 2.5. Average yield, coefficient of variation of yield (*cv*), CPUE, and risk for four policies of apportionment of sablefish catch limits. Yield and CPUE are expressed relative to the maximum for a particular hypothesis.

Area	*Hypothesis*															
		A				*B*				*C*				*Average*			
	Policy	*Yield*	*CV*	*CPUE*	*Risk*	*Yield*	*CV*	*CPUE*	*Risk*	*Yield*	*CV*	*CPUE*	*Risk*	*Yield*	*CV*	*CPUE*	*Risk*
EG	1	0.19	0.20	1.00	0.07	0.19	0.20	1.00	0.05	0.20	0.20	1.00	0.04	0.20	0.20	1.00	0.06
	2	0.42	0.21	0.94	0.10	0.46	0.21	0.93	0.09	0.52	0.21	0.90	0.08	0.46	0.21	0.92	0.09
	3	0.41	0.18	0.94	0.10	0.46	0.18	0.93	0.09	0.52	0.18	0.90	0.08	0.46	0.18	0.92	0.09
	4	0.41	0.19	0.94	0.10	0.45	0.19	0.93	0.08	0.51	0.19	0.90	0.08	0.46	0.19	0.92	0.09
CG	1	0.19	0.20	0.59	0.05	0.19	0.20	0.57	0.05	0.20	0.20	0.51	0.05	0.20	0.20	0.56	0.05
	2	0.25	0.22	0.60	0.05	0.27	0.22	0.57	0.05	0.27	0.22	0.49	0.06	0.27	0.22	0.55	0.05
	3	0.25	0.20	0.60	0.05	0.27	0.20	0.57	0.05	0.27	0.20	0.49	0.06	0.27	0.20	0.55	0.05
	4	0.26	0.19	0.60	0.05	0.27	0.19	0.57	0.05	0.27	0.19	0.49	0.06	0.27	0.19	0.55	0.05
WG	1	0.19	0.20	0.60	0.11	0.19	0.20	0.50	0.13	0.20	0.20	0.38	0.15	0.20	0.20	0.49	0.13
	2	0.15	0.22	0.69	0.04	0.15	0.22	0.59	0.04	0.13	0.22	0.45	0.06	0.14	0.22	0.56	0.05
	3	0.15	0.21	0.68	0.04	0.15	0.21	0.59	0.04	0.13	0.21	0.45	0.06	0.14	0.21	0.56	0.05
	4	0.15	0.19	0.68	0.04	0.15	0.19	0.59	0.05	0.13	0.19	0.45	0.06	0.14	0.19	0.56	0.05
BS	1	0.19	0.20	0.07	0.14	0.19	0.20	0.03	0.29	0.20	0.20	0.02	0.46	0.20	0.20	0.04	0.30
	2	0.05	0.28	0.08	0.02	0.04	0.28	0.05	0.03	0.02	0.28	0.03	0.05	0.04	0.28	0.05	0.03
	3	0.05	0.27	0.08	0.02	0.04	0.27	0.05	0.03	0.02	0.27	0.03	0.06	0.04	0.27	0.05	0.04
	4	0.05	0.19	0.08	0.03	0.04	0.19	0.05	0.03	0.02	0.19	0.03	0.06	0.04	0.19	0.05	0.04
AL	1	0.19	0.20	0.09	0.14	0.19	0.20	0.04	0.41	0.20	0.20	0.02	0.89	0.20	0.20	0.05	0.48
	2	0.13	0.25	0.11	0.02	0.09	0.25	0.07	0.03	0.06	0.25	0.04	0.06	0.09	0.25	0.07	0.04
	3	0.13	0.24	0.11	0.02	0.09	0.24	0.07	0.03	0.06	0.24	0.04	0.06	0.09	0.24	0.07	0.04
	4	0.13	0.19	0.11	0.03	0.09	0.19	0.07	0.04	0.06	0.19	0.04	0.06	0.09	0.19	0.07	0.04
All areas combined	1	0.97	0.09	0.47	0.07	0.97	0.09	0.43	0.07	1.00	0.09	0.38	0.07	0.98	0.09	0.43	0.07
	2	1.00	0.11	0.67	0.05	1.00	0.12	0.67	0.06	1.00	0.13	0.66	0.07	1.00	0.12	0.66	0.06
	3	1.00	0.10	0.67	0.05	1.00	0.11	0.67	0.06	1.00	0.12	0.66	0.07	1.00	0.11	0.66	0.06
	4	1.00	0.10	0.66	0.06	1.00	0.11	0.67	0.06	1.00	0.12	0.66	0.07	1.00	0.11	0.66	0.06

EG, Eastern Gulf of Alaska; CG, Central Gulf of Alaska; WG, Western Gulf of Alaska; BS, Eastern Bering Sea; AL, Aleutians.

maintained by migrants from other areas and not by recruitment as hypothesized by Sasaki (1985) and Beamish and McFarlane (1988), then fisheries in the westward areas may benefit from low overall exploitation rates. Conversely, if recruitment occurs throughout the northeastern Pacific Ocean, then fisheries in the eastern areas will benefit from low overall fishing rates. Future analyses should focus on estimating the geographical distribution of recruitment from age-composition data collected during surveys.

In our study, yield-per-recruit was evaluated under one apportionment strategy and with constant overall recruitment. A more comprehensive analysis of yield-per-recruit should include the analysis of the alternative policies and alternative stock and recruitment relationships. In our results, we presented an evaluation of apportionment policies with the current estimated exploitation rate of 10%. We have also evaluated these policies with considerably higher exploitation rates (ie. 20% and 30%) and the results were qualitatively similar.

Selection of the most appropriate apportionment policy is unclear, because a particular policy did not dominate across all hypotheses and attributes. The result that policies 2-4 performed similarly across all attributes is because, on average, the apportionments for these three policies are similar. Policy 1 had the lowest overall variability in yield but substantially higher risk in the westward areas and lowest overall CPUE. If an objective is to optimize CPUE and maintain spawning biomass on an areal basis, then policy 1 is not appropriate. Given the uncertainty about the location of spawning areas for sablefish, a policy that maintains spawning biomass in each area is desirable.

Policies 2 and 3 have some appealing attributes. They adapt to current information about geographical distribution of available biomass and do not require estimates of movement rates for implementation. Policy 3 tends to result in less variable yields than policy 2 because policy 3 is less sensitive than policy 2 to annual fluctuations

in biomass estimates due to measurement error. For policy 3, the most recent year is given a weight of two and the prior four years are given a weight of one. This weighting scheme has been chosen somewhat arbitrarily and alternative weighting schemes may be more appropriate. If the method of weighting is based on the ratio of survey measurement error to total variability (i.e., measurement error plus variability in natural mortality, recruitment, and movement rates), then an exponential weighting scheme is appropriate (Meinhold and Singpurwalla, 1983). [3]

Policy 4 does not depend on biomass estimation on an areal basis for implementation, but does require knowledge of movement patterns. In our analysis, we assumed no error in information about movement patterns and that movement patterns change with age but do not change over time. There is considerable uncertainty about the estimates of movement rates used in this study (Heifetz and Fujioka, 1991[chapter 1]). In addition, movement rates may exhibit some temporal variability. Temporal shifts in movement rates may be related to population abundance, environmental factors, or food abundance (Beverton and Holt, 1957; MacCall, 1990; Polacheck, 1990).

We do not examine the determination of an optimal policy of apportionment of the catch limit among regulatory areas, which requires the definition of a function that incorporates the objectives of fishery management such as maximizing yield and minimizing yield variability and risk (e.g., Quinn *et al.*, 1990b). Geographic optimization of harvest can produce higher sustained yields than harvests without geographic restrictions (MacCall, 1990).

In conclusion, for populations that have high mixing rates among geographic areas, such as sablefish in the northeastern Pacific Ocean, an apportionment policy that is based on the geographic distribution of estimated biomass is reasonable (policies 2 and 3). In general, such policies are robust to alternative recruitment hypotheses. For implementation, such policies require estimates of biomass but do not require estimates

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[3]This method of weighting was adopted by the NPFMC for the 1995-96 sablefish fishery.

of movement rates. The current apportionment policy for sablefish (policy 3) also reduces the effects of annual fluctuations in biomass estimates due to measurement error. Applying our techniques to other migratory populations may prove worthwhile. Modifications such as the inclusion of a functional stock and recruitment relationship or variability in movement rates should be examined.

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Chapter 3.
Dynamics of an Age-by-region Fish Population Model

Abstract

The reproduction, mortality and migration of an age-structured fish population can be incorporated into a matrix model. The population projection matrix for such a model describes the dynamics of age classes within regions and the migration among regions. Such a model provides a flexible framework to examine the dynamics of a migratory fish population. The model can be parameterized to include regional specificity in the stock-recruitment relationship as well as larval dispersal that is decoupled from local reproduction. Methods to examine equilibrium, stability, and transient properties of the model are described. The subject of oriented movement, where young fish tend to migrate in the opposite direction of older fish is examined within the context of the sablefish (*Anoplopoma fimbria*) fishery in the northeast Pacific Ocean. We show that fishing at a common rate among regions may be appropriate for the pooled population but may be detrimental to the population in a given region. As an alternative, region-specific fishing strategies can be devised to meet fishery management objectives such as maintenance of regional spawning potential.

Introduction

The processes of reproduction, survival, and migration of an age-structured population can be formulated within the basic framework of matrix models described in Caswell (1989) and Getz and Haight (1989). Such a model is a natural extension of the Leslie (1945) matrix population model. First described by Rogers (1966; 1985), the model has been used extensively to analyze regional aspects of human populations (Liaw, 1980) and has occasionally been applied to plants, fish, and wildlife (e.g., Fujioka, 1978; Lande, 1988). The underlying feature of such models is that all demographic features of a population can be formulated within a projection matrix. This formulation allows the use of some of the theoretical generalities for stage-structured models (Caswell, 1989).

In this paper we first present a general structure for modeling the dynamics of a migratory age-structured fish population subject to exploitation. After presenting the mathematical description of the general model structure, we present methods to examine equilibrium, stability, and transient properties of the model. Then we present an application of the model with hypothetical data and within the context of the sablefish (*Anoplopoma fimbria*) population in the northeast Pacific Ocean. An example of how the model can be used for management of the sablefish fishery is presented. For fisheries that occur in different geographic areas, are prosecuted by different user groups, and in some instances may cross international boundaries, knowledge of how a fishery in one area interacts with another may lead to improved management.

Model Specification

The General Age-by-region Model

The stage-classified matrix model described in Caswell (1989) forms the basis for this model. In our paper the formulation is translated into that commonly used for age-

structured fish populations (e.g., Quinn and Szarzi, 1993). In our notation variables in bold denote matrices or vectors. Let

$N_{a,t,i}$ = abundance at age a, year t, and region i.
$\theta_{a,t}(i \rightarrow k)$ = migration proportion from region i to k at age a and year t.
K = number of regions.
A = oldest age.
$f_{a,i}$ = net fecundity at age a and region i.
M = instantaneous rate of natural mortality.
$s_{a,i}$ = fishery selectivity at age a and region i.
$F_{t,i}$ = rate of full-recruitment fishing mortality (i.e., s_a=1) in year t and region i.
$Z_{a,t,i} = M + s_{a,i} F_{t,i}$ = total instantaneous mortality at age a, year t, and region i.
$S_{a,t,i} = \exp(-Z_{a,t,i})$ = survival at age a, year t, and region i.
r = recruitment age and usually first appearance of fish in the database.

Note that $\sum_{k=1}^{K} \theta_{a,t}(i \rightarrow k) = 1$ and that the probability of staying in the same region $\theta_{a,t}(i \rightarrow i) = 1 - \sum_{k \neq i}^{K} \theta_{a,t}(i \rightarrow k)$. In our formulation absence of age or region subscripts for abundance denotes summation over the missing subscript, and absence of a time subscript denotes equilibrium (i.e., $t \rightarrow \infty$). For other model parameters absence of a subscript indicates the parameter is constant over the missing subscript.

The assumptions for such a model are generally the same as that for many age-structured fishery models (e.g., Deriso *et al.*, 1985) with the added dimension of region (Quinn *et al.*, 1990). Fishing mortality $F_{a,t,i}$ is assumed to be separable ($s_{a,i}F_{t,i}$) into an age factor ($s_{a,i}$) and a year factor ($F_{t,i}$) for each region where age selectivity $s_{a,i}$ is equal to 1 for at least one fully recruited age. Natural mortality M is assumed to be constant, although the model can be easily altered to accommodate age, year, and region specific M. Migration rates $\theta_{a,t}(i \rightarrow k)$ are assumed to depend on age, year, and region. The migration process is assumed to be Markovian because for a given year and region all fish of the same age have the same migration probabilities regardless of their previous history. Net fecundity $f_{a,i}$ is assumed to depend on age and region and is computed from the product of proportion of females mature at age and fecundity of a mature female at age.

Alternate formulations of the model are conceptually possible such as age-, year-, and region-specific natural mortality, year-specific fecundity and selectivity, and migration rates that depend on year class, population density, or season. Migration is assumed to occur instantaneously just after the start of a year followed by natural and fishing mortality.

The basic recursive equation that describes the dynamics of the population is

New population = survival [*old population* - *emigration* + *immigration*]

$$N_{a+1,t+1,i} = S_{a,t,i}\left[N_{a,t,i} - N_{a,t,i}\sum_{k\neq i}^{K}\theta_{a,t}(i\to k) + \sum_{k\neq i}^{K} N_{a,t,k}\theta_{a,t}(k\to i)\right]$$

$$= S_{a,t,i}\left[N_{a,t,i}\{1 - \sum_{k\neq i}^{K}\theta_{a,t}(i\to k)\} + \sum_{k\neq i}^{K} N_{a,t,k}\theta_{a,t}(k\to i)\right]. \quad (3.1)$$

Equation (3.1) simplifies to

$$N_{a+1,t+1,i} = S_{a,t,i}\sum_{k=1}^{K}\theta_{a,t}(k\to i)N_{a,t,k} \quad (3.2)$$

because the term in { } is just $\theta_{a,t}(i\to i)$. From the Baranov catch equation, the exploitation fraction is

$$\mu_{a,t,i} = \frac{s_{a,t,i}F_{t,i}}{Z_{a,t,i}}(1 - \exp(-Z_{a,t,i})). \quad (3.3)$$

Hence from (3.2), catch is

$$C_{a,t,i} = \mu_{a,t,i}\sum_{k=1}^{K}\theta_{a,t}(k\to i)N_{a,t,i}. \quad (3.4)$$

Egg production in year t and region i is

$$N_{0,t,i} = \sum_{a=1}^{A} f_{a,i} N_{a,t,i} , \qquad (3.5)$$

which assumes that egg production takes place at the start of the year before migration. In the absence of migration during the early life stages, the relationship between recruitment and egg production can be written

$$N_{r,t+r,i} = l_{r,i} N_{0,t,i} \psi_i(N_{0,t,i}) \qquad (3.6)$$

where $l_{r,i}$ is early life survival from age 0 up to recruitment age r without density dependence and $\psi_i(N_{0,t,i})$ is a function representing density dependence in a region. If, however, recruitment is decoupled from local reproduction by movement (e.g., dispersal of planktonic larvae or movement of pre-recruits), then

$$N_{r,t+r,i} = l_{r,i} \sum_{k=1}^{K} N_{0,t,k} \psi_k (N_{0,t,k}) \theta_{0,t}(k \to i), \qquad (3.7)$$

which assumes that density dependence precedes dispersal, and dispersal occurs up to the recruitment age r followed by survival. Note that equation (3.7) is the same as (3.6) if $\theta_{0,t}(i \to k) = 0$ for $k \neq i$ and $\theta_{0,t}(i \to k) = 1$ for $k = i$. Equation (3.7) assumes that all dispersion occurs right after egg production. This may not be a realistic assumption. A more complex model that incorporates physical factors such as oceanographic currents can model dispersion more realistically (e.g., Possingham and Roughgarden, 1990), but the simpler model may be adequate.

Putting the model described in (3.1) - (3.7) in the form of a projection matrix is a convenient way of examining the dynamics of such a model (Caswell, 1989). Given the vector of abundance at age and region N_t, the matrix $\boldsymbol{P}_t$ in the equation

$$N_{t+1} = \boldsymbol{P}_t N_t \qquad (3.8)$$

is the projection matrix. As an example consider the hypothetical example of three age groups and three regions, without density dependence, without migration during early life stages, and constant fecundity, survival and migration over time. The projection matrix $\boldsymbol{P}$ is

$$\boldsymbol{P} = \begin{pmatrix} l_1 f_{1,1} & l_1 f_{2,1} & l_1 f_{3,1} & 0 & 0 & 0 & 0 & 0 & 0 \\ S_{1,1}\theta_1(1-1) & 0 & 0 & S_{1,1}\theta_1(2-1) & 0 & 0 & S_{1,1}\theta_1(3-1) & 0 & 0 \\ 0 & S_{2,1}\theta_2(1-1) & 0 & 0 & S_{2,1}\theta_2(2-1) & 0 & 0 & S_{2,1}\theta_2(3-1) & 0 \\ 0 & 0 & 0 & l_2 f_{1,2} & l_2 f_{2,2} & l_2 f_{3,2} & 0 & 0 & 0 \\ S_{1,2}\theta_1(1-2) & 0 & 0 & S_{1,2}\theta_1(2-2) & 0 & 0 & S_{1,2}\theta_1(3-2) & 0 & 0 \\ 0 & S_{2,2}\theta_2(1-2) & 0 & 0 & S_{2,2}\theta_2(2-2) & 0 & 0 & S_{2,2}\theta_2(3-2) & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & l_3 f_{1,3} & l_3 f_{2,3} & l_3 f_{3,3} \\ S_{1,3}\theta_1(1-3) & 0 & 0 & S_{1,3}\theta_1(2-3) & 0 & 0 & S_{1,3}\theta_1(3-3) & 0 & 0 \\ 0 & S_{2,3}\theta_2(1-3) & 0 & 0 & S_{2,3}\theta_2(2-3) & 0 & 0 & S_{2,3}\theta_2(3-3) & 0 \end{pmatrix}.$$

where the population vector for abundance N_t can be written as

$$\boldsymbol{N_t} = \begin{pmatrix} N_{1,1,1} \\ N_{2,1,1} \\ N_{3,1,1} \\ N_{1,2,2} \\ N_{2,2,2} \\ N_{3,2,2} \\ N_{1,3,3} \\ N_{2,3,3} \\ N_{3,3,3} \end{pmatrix}.$$

The entries in the first, fourth, and seventh rows of $\boldsymbol{P}$ are termed the fertility coefficients and the other entries are termed the survival-migration coefficients. To introduce migration and/or density dependence at early life stages requires modification

of the fertility coefficients. For example from equations (3.6) and (3.7) the element $P_{1,1}$ (row 1, column 1) is

$$\begin{aligned} P_{1,1} &= l_1 f_{1,1} \psi_1 \left(\sum_{a=1}^{A} f_{a,1} N_{a,t,1} \right) \theta_0(1-1) \\ &= l_1 f_{1,1} \psi_1(N_{0,t,1}) \theta_0(1-1), \end{aligned}$$

and the element $P_{1,4}$ (row 1, column 4) is

$$P_{1,4} = l_1 f_{1,2} \psi_2(N_{0,t,2}) \theta_0(2-1).$$

With the addition of density dependence, this is no longer a constant linear Leslie matrix because elements of $\boldsymbol{P}$ are now functions of abundance and ψ can be any function.

Traditional Leslie Matrix Model

Equations (3.2) and (3.5) are equivalent to the traditional Leslie matrix model with migration when $\psi(x) = 1$, and survival, fecundity, and migration are constant over time. Note that Caswell (1989; Chapter 4) describes this model extensively. Here we provide a brief summary.

Examination of the eigenvalues (λ_i) of $\boldsymbol{P}$ provides information on the asymptotic dynamics of the population. Given an initial population, the growth of the population can be decomposed into a set of exponential contributions that depends on the magnitude $|\lambda_i|$ of each eigenvalue. If $|\lambda_i| < 1$, its contribution to population growth decays, smoothly if $\lambda_i > 0$, with oscillations if $\lambda_i < 0$ or if λ_i is complex. If $|\lambda_i| > 1$, its contribution to population growth grows exponentially, smoothly if $\lambda_i > 0$, with oscillations if $\lambda_i < 0$ or if λ_i is complex.

Under certain regularity conditions and regardless of the initial population, the population will eventually grow at a rate given by the dominant eigenvalue λ_1 and reach a stable age/region distribution. The dominant eigenvalue is a real number that is strictly greater in magnitude than any other eigenvalue. Depending on the value of λ_1, the population pooled over regions and ages will exponentially increase ($\lambda_1 > 1$), decrease ($\lambda_1 < 1$), or remain the same ($\lambda_1 = 1$). The stable age/region distribution is proportional to the right eigenvector corresponding to λ_1.

The rate a population will converge to the stable distribution is governed by the relationship between λ_1 and the eigenvalue with the second largest magnitude $|\lambda_2|$ (Caswell, 1989). The damping ratio ρ is defined as

$$\rho = \frac{\lambda_1}{|\lambda_2|}.$$

Convergence will be more rapid the larger ρ is. Within the context of age by region models there are two levels of convergence: the regional distribution and the age distribution. Whether the age distribution converges more or less rapidly than the region distribution seems to depend on the details of the model and may be related to the magnitudes of the subdominant eigenvalues of the matrix (Caswell, 1989).

A special simple case of this model is when survival and fecundity are constant among regions. For this special case from equation (3.2), population abundance at age summed over regions is

$$N_{a+1,t+1} = S_a \sum_{i=1}^{K} N_{a,t,i} = S_a N_{a,t} ,$$

and from equation (3.7) abundance of recruits at age r summed over regions is

$$N_{r,t+1} = l_r \sum_{i=1}^{K} \sum_{a=r}^{A} f_a N_{a,t,i} = l_r \sum_{a=r}^{A} f_a N_{a,t}$$

These equations define the traditional Leslie matrix model for a population combined over regions.

Density Dependence

In the previous section we presented a model for a migratory age-structured population in which recruitment is proportional to population abundance. For many populations such a model is not adequate because the population can decrease or increase exponentially unless $\lambda_t = 1$. A more realistic model can be formulated by inclusion of density dependence to account for non-linearity in the relationship between egg-production and recruitment. Density dependence can result in a stationary population and stable age-by-region structure, or in complex behavior such as limit cycles and chaotic fluctuations (Caswell, 1989). A good general description of the types of population dynamics that can result from non-linear models is in Nisbet and Gurney (1982).

At least three alternative cases of the process of regional density dependence can be hypothesized. We formulate these cases in the absence of migration at early life stages, but they can be easily adapted for the more complex model.

Case 1: Density-dependent effects within a region are from the population as a whole, with the same stock-recruitment relationship among regions. From equation (3.6) this case can be written

$$\text{Case 1:} \qquad N_{r,t+r,i} = l_r N_{0,t,i}\, \psi\left(\sum_{k=1}^{K} N_{0,t,k}\right) = l_r N_{0,t,i}\, \psi(N_{0,t}) .$$

In this case the stock-recruitment relationship represents the entire population pooled over regions. Early life survival in the absence of density dependence and the level of density dependence are independent of region. Such a model results in recruits being

apportioned to a given region in direct proportion to the number of eggs produced in a given region.

Case 2: Density-dependent effects are from the population in a region with the same stock-recruitment relationship among regions such that

$$\text{Case 2:} \qquad N_{r,t+r,i} = l_r N_{0,t,i}\, \psi(N_{0,t,i}).$$

For this case, offspring produced from eggs in all regions have the same early life survival in the absence of density dependence, but the level of density dependence is influenced by the number of eggs produced within a specific region.

Case 3: Density-dependent effects are from the population in a region with different stock-recruitment relationships among regions. The formulation for such a case is given by equation (3.6)

$$\text{Case 3:} \qquad N_{r,t+r,i} = l_{r,i} N_{0,t,i}\, \psi_i(N_{0,t,i}).$$

For this case early life survival in the absence of density dependence is region-specific and the level of density dependence depends on the number of eggs produced within a region and the region where the eggs are produced.

Equilibria

At equilibrium the population vector $\boldsymbol{N}$ satisfies the condition that

$$\boldsymbol{N} = \boldsymbol{P}_N \boldsymbol{N}. \qquad (3.9)$$

The notation $\boldsymbol{P}_N$ indicates that the projection matrix depends on the population vector $\boldsymbol{N}$. A special situation for Case 1 is where survival and fecundity are the same in each region.

The fertility coefficients for such a situation are independent of the region, and the solution to the equilibrium population follows directly from the formulae for a population without regional structure as in Quinn and Szarzi (1993) (also in Caswell (1989) and Getz and Haight (1989)). Assume that the age of recruitment r is young enough so that no younger fish are mature and $\psi(x)$ is an invertible function. Let

$$L_a = \prod_{x=r}^{a-1} S_x$$
$$E_r = \sum_{a=r}^{A} f_a L_a$$
$$R_0 = l_r E_r .$$

L_a is the cumulative survival from age r to age a, E_r is the lifetime egg production of an r year old, and R_0 is surviving egg production to age r. Note that in our notation E_r is substituted for P_r of Quinn and Szarzi (1993). Equilibrium egg production N_0, number of recruits N_r, and numbers at age N_a, summed over regions are given by

$$N_0 = \psi^{-1}\left(\frac{1}{l_r E_r}\right) = \psi^{-1}\left(\frac{1}{R_0}\right)$$
$$N_r = l_r N_0 \psi(N_0) = \frac{l_r N_0}{R_0} = \frac{N_0}{E_r}$$
$$N_a = N_r L_a .$$

For the Ricker stock-recruitment function [i.e., $\psi(N_0) = \exp(-\beta N_0)$]

$$N_0 = \frac{1}{\beta}\ln(R_0),$$

and for the Beverton-Holt stock-recruitment function [i.e, $\psi(N_0) = (1 + \beta N_0)^{-1}$] (Getz and Haight, 1989)

$$N_0 = \frac{R_0 - 1}{\beta} .$$

Given v, the dominant right eigenvector of $\boldsymbol{P}_N$ that has been normalized to sum to one, the equilibrium population vector is

$$\boldsymbol{N} = N\boldsymbol{v}.$$

The elements of $\boldsymbol{v}$ (i.e.,$\{v_{i,a}\}$) give the proportions of the population at a given age and region.

If the fertility coefficients and/or survival differ among regions, the simple equations for the population pooled over regions cannot be used to determine the equilibrium population. We are not aware of any studies that have estimated N for such a case and multiple equilibria may be possible (Caswell, 1989). The abundance at age in a region can be written

$$N_{a,i} = Nv_{a,i} .$$

If $Nv_{a,i}$ is substituted for $N_{a,i}$, equation (3.5) becomes

$$N_{0,i} = N\sum_{a=1}^{A} f_{a,i}v_{a,i}$$

and then equation (3.6) becomes

$$v_{r,i} = l_{r,i}\left(\sum_{a=1}^{A} f_{a,i}v_{a,i}\right)\psi_i\left(N\sum_{a=1}^{A} f_{a,i}v_{a,i}\right) . \qquad (3.10)$$

Let

$$\eta_i = \frac{v_{a,i}}{l_{r,i}\sum_{a=1}^{A} f_{a,i} v_{a,i}}$$

Solving for N in equation (3.10),

$$N = \frac{\psi_i^{-1}(\eta_{a,i})}{\sum_{a=1}^{A} f_{a,i} v_{a,i}}$$

This implies that to solve for N requires that $v_{a,i}$ be known, but $v_{a,i}$ depends on N so that the utility of this approach may not be of practical relevance.

A closed form solution can be found that will enable the equilibrium population to be solved for. Let $\boldsymbol{P}^*$ denote a $(A - r)$ by $(A - r)$ submatrix of $\boldsymbol{P}$ composed of the survival-migration coefficients (i.e., $\boldsymbol{P}_a^* = \{S_{a,i}\theta_a(i \to k)\}$) for each age a. Since $\boldsymbol{P}_a^*$ does not contain the fertility coefficients, it is independent of N. Given an initial vector of abundance at age of recruitment r in year t, $N_{r,t}$, the vector of abundance at age a in year t is

$$\begin{aligned} \boldsymbol{N}_{a,t} &= \boldsymbol{P}_a^* \cdots\cdots \boldsymbol{P}_r^* \boldsymbol{N}_{r,t-a+r} \\ &= \left(\prod_{x=r}^{a-1} \boldsymbol{P}_x^* \right) N_{r,t-a+r}. \end{aligned}$$

Thus from the definition of matrix multiplication the abundance at age in region i can be written

$$N_{a,t,i} = \sum_j p_{i,j}(a) N_{r,t-a+r,j},$$

where the notation $p_{i,j}(a)$ denotes the (i,j) entry of $\prod \boldsymbol{P}_r^*$. Note that if $a = r$ then $\prod \boldsymbol{P}^*$ is replaced by the identity matrix. Dropping time subscripts to obtain equilibrium results in

$$N_{a,i} = \sum_j p_{i,j}(a) N_{r,j}.$$

From equation (3.5)

$$N_{0,i} = \sum_a \sum_j f_{a,i}\, p_{i,j}(a) N_{r,j}$$

so that from equation (3.6)

$$N_{r,i} = l_{r,i} \sum_a \sum_j f_{a,i}\, p_{i,j}(a) N_{r,j}\, \psi_i\left(\sum_a \sum_j f_{a,i}\, p_{i,j}(a) N_{r,j} \right). \quad (3.11)$$

Since there are K (i.e., regions) such equations and K unknowns (i.e, the $N_{r,i}$'s), the equilibrium abundance can be solved for with non-linear optimization computer software.

An alternative way to estimate the equilibrium population is by the power method. One begins with an arbitrary vector of abundance and multiplies by $\boldsymbol{P}_N$ repeatedly until the population stabilizes. Note that $\boldsymbol{P}_N$ is updated each time the multiplication is performed because $\boldsymbol{P}_N$ depends on $\boldsymbol{N}$.

Stability Analysis

Existence of an equilibrium does not guarantee its stability. For unstable equilibria the population does not converge to the original $\boldsymbol{N}$ if a parameter is varied for some time and then returned to its original value. For a special situation of Case 1 where survival and fecundity are constant among regions, a stable equilibrium for the Ricker function exists when $1 < R_0 < e^2$ and for the Beverton-Holt function a stable equilibrium

always exists (Getz and Haight, 1989). Derivation of the stability properties of the equilibrium for the other cases can be accomplished by adapting the methods of Beddington (1974) and Levin (1981), described in Emlen (1984) and Caswell (1989). The local stability properties of N are determined by the eigenvalues of the linear approximation matrix $\boldsymbol{B}$. Given the equilibrium vector of abundance N^* for the age-by-region model,

$$\boldsymbol{B} = \boldsymbol{P}_{N^*} + \sum_{m}^{M} \left. \frac{\partial \boldsymbol{P}}{\partial N_m} \right|_{N^*} \boldsymbol{H}_m , \qquad (3.12)$$

where $\boldsymbol{H}_m$ has N^* in column m and zeros elsewhere. If the magnitude of the maximum eigenvalue of $\boldsymbol{B}$ is less than 1, the equilibrium point is asymptotically stable, if greater than 1 the equilibrium point is unstable. In addition, if any of the eigenvalues is negative the population cycles. The $\{i,j\}$ element of $\boldsymbol{B}$ is

$$B_{i,j} = P_{i,j}(N^*) + \sum_{m=1}^{M} \left. \frac{\partial P_{i,m}}{\partial N_m} \right|_{N^*} N_m^* ,$$

where $M = K(A - r + 1)$. For our parameterization of the age-region model, the only terms that depend on N are the fertility coefficients. Thus, examination of stability properties requires differentiation of the fertility coefficients evaluated at the equilibrium N^*. For the elements of $\boldsymbol{P}$ with the fertility coefficients,

$$\frac{\partial P_{i,j}}{\partial N_{a,k}} = \frac{\partial}{\partial N_{a,k}} [l_{r,k} f_{a,k} \psi_k(N_{0,k})] = l_{r,k} f_{a,k} g ,$$

where

$$g = \frac{\partial}{\partial N_{0,k}}[\psi_k(N_{0,k})]\Big|_{N_{0,k}^{\cdot}} .$$

For Case 3 and the Ricker model

$$g = \frac{\partial}{\partial N_{0,k}}[\exp(-\beta_k N_{0,k})]\Big|_{N_{0,k}^{\cdot}}$$
$$= -\beta_k f_{a,k}\exp(-\beta_k N_{0,k}^{\cdot})$$

so that

$$\frac{\partial P_{i,j}}{\partial N_{a,k}} = -\beta_k \alpha_k f_{a,k}^2 \exp(-\beta_k N_{0,k}^{\cdot}) .$$

The proper equations to analyze the stability properties for other cases and other stock-recruitment functions can be similarly determined.

Application of the Model

Hypothetical Example

Consider a population with three ages (i.e., $A = 3$), two regions (i.e., $K = 2$), density dependence defined by Case 3 of the Ricker stock-recruitment relationship, and the following time invariant parameters:

$\theta_{a,t}(i \to k) = \{0.4, 0.2\}$ for $a = \{1, 2\}$, $i = 1$, and $k = 2$;
$\theta_{a,t}(i \to k) = \{0.5, 0.3\}$ for $a = \{1, 2\}$, $i = 2$, and $k = 1$;
$f_{a,i} = \{10, 20, 30\}$ for $a = \{1, 2, 3\}$ and $i = 1$;
$f_{a,i} = \{20, 30, 40\}$ for $a = \{1, 2, 3\}$ and $i = 2$;
$M = 0.1$; $r = 1$;

$s_{a,i}$ = {0.5, 1.0} for a = {1, 2} and i =1;
$s_{a,i}$ = {0.7, 1.0} for a = {1, 2} and i =2;
F_i = {0.1,0.2} for i = {1,2};
α_i = {0.20, 0.15} for i = {1,2};
β_i = {0.0001, 0.0002} for i = {1,2};

Thus, $S_{a,i}$ = {0.86, 0.82} for a = {1, 2} and i = 1 and $S_{a,i}$ = {0.79, 0.74} for a = {1, 2} and i = 2. The projection matrix is given by

$$\boldsymbol{P}_{N_t} = \begin{pmatrix} \alpha_1 f_{1,1}\exp(-\beta_1 N_{0,t,1}) & \alpha_1 f_{2,1}\exp(-\beta_1 N_{0,t,1}) & \alpha_1 f_{1,1}\exp(-\beta_1 N_{0,t,1}) & 0 & 0 & 0 \\ S_{1,1}\theta_1(1-1) & 0 & 0 & S_{1,1}\theta_1(2-1) & 0 & 0 \\ 0 & S_{2,1}\theta_2(1-1) & 0 & 0 & S_{2,1}\theta_2(2-1) & 0 \\ 0 & 0 & 0 & \alpha_2 f_{1,2}\exp(-\beta_2 N_{0,t,2}) & \alpha_2 f_{2,2}\exp(-\beta_2 N_{0,t,2}) & \alpha_2 f_{1,2}\exp(-\beta_2 N_{0,t,2}) \\ S_{1,2}\theta_1(1-2) & 0 & 0 & S_{1,2}\theta_1(2-2) & 0 & 0 \\ 0 & S_{2,2}\theta_2(1-2) & 0 & 0 & S_{2,2}\theta_2(2-2) & 0 \end{pmatrix}$$

$$= \begin{pmatrix} 2\exp(-0.0001N_{0,t,1}) & 4\exp(-0.0001N_{0,t,1}) & 6\exp(-0.0001N_{0,t,1}) & 0 & 0 & 0 \\ 0.516 & 0 & 0 & 0.430 & 0 & 0 \\ 0 & 0.656 & 0 & 0 & 0.246 & 0 \\ 0 & 0 & 0 & 3\exp(-0.0002N_{0,t,2}) & 4.5\exp(-0.0002N_{0,t,2}) & 6\exp(-0.0002N_{0,t,2}) \\ 0.316 & 0 & 0 & 0.395 & 0 & 0 \\ 0 & 0.148 & 0 & 0 & 0.518 & 0 \end{pmatrix}$$

The $\boldsymbol{P}$* matrices are

$$\boldsymbol{P}_1^* = \begin{pmatrix} 0.516 & 0.430 \\ 0.316 & 0.395 \end{pmatrix}, \quad \boldsymbol{P}_2^* = \begin{pmatrix} 0.656 & 0.296 \\ 0.148 & 0.518 \end{pmatrix},$$

and their product is

$$\prod_{x=1}^{2} \boldsymbol{P}_x^{\bullet} = \boldsymbol{P}_2^{\bullet}\boldsymbol{P}_1^{\bullet} = \begin{pmatrix} 0.416 & 0.379 \\ 0.240 & 0.268 \end{pmatrix}$$

for $x = 0$, $x = 1$, and $x = 2$, respectively.

Figure 3.1 shows the projection of population starting with an initial population at $t = 1$ in region 1 of $N_{a,1,1} = \{50, 40, 30\}$ for $a = \{1, 2, 3\}$, and in region 2 of $N_{a,1,2} = \{100, 90, 80\}$ for $a = \{1, 2, 3\}$. The age classes in each region undergo damped oscillations until convergence to an equilibrium. The equilibrium population computed analytically using equation (3.11) is

$$\boldsymbol{N}^{\bullet} = \begin{pmatrix} 542 \\ 327 \\ 268 \\ 111 \\ 215 \\ 160 \end{pmatrix}$$

which is identical to the equilibrium population determined via the power method (i.e., $t = 40$ in Figure 3.1). Most of the oscillatory behavior of the population was due to fluctuations among age classes (Figure 3.1). The regional distribution converged rapidly with small oscillations.

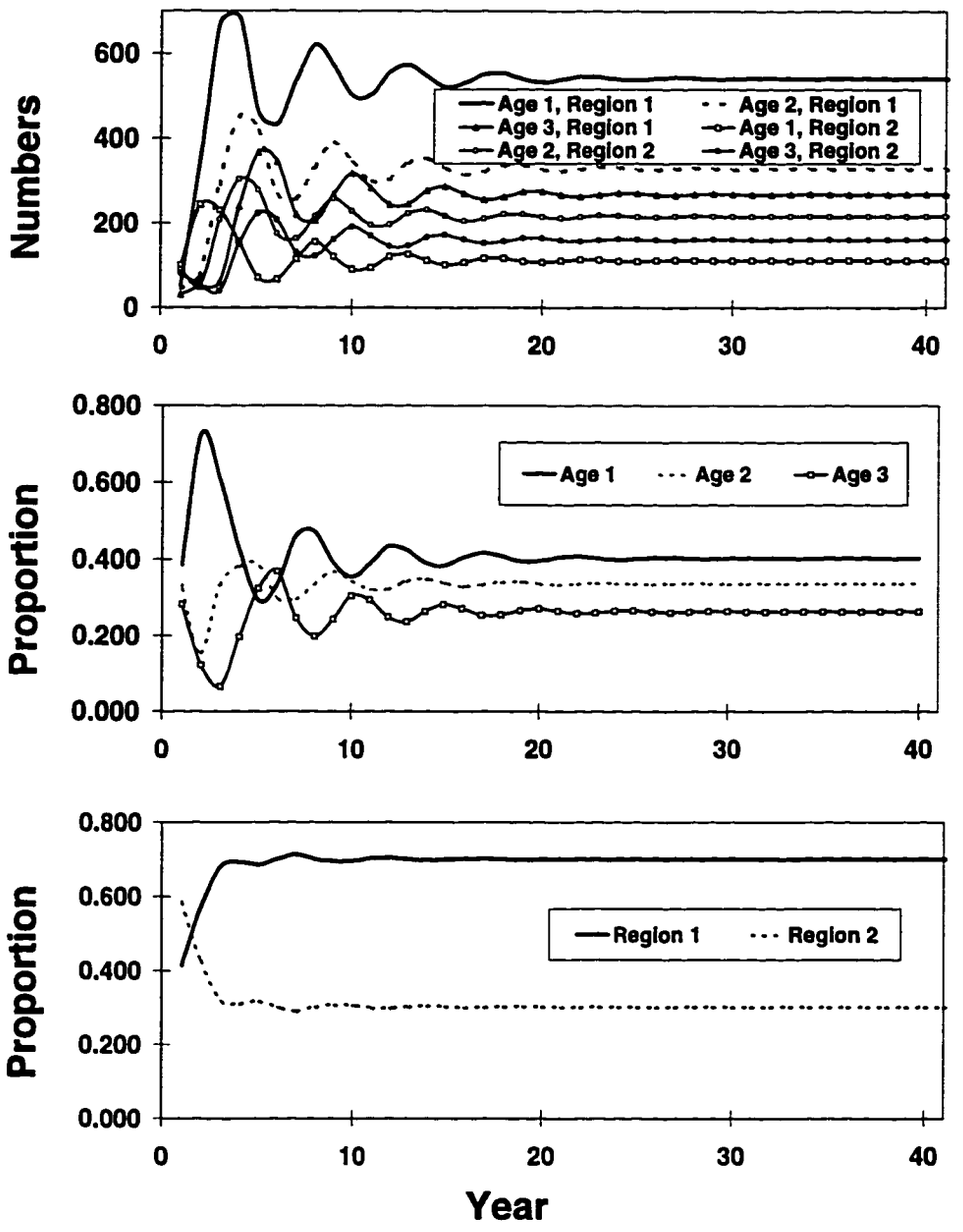

Figure 3.1. Projection of a hypothetical fish population based on the age-by-region model with density dependence defined with $(\alpha, \beta) = (0.20, 0.0001)$ and $(0.15, 0.0002)$ for region 1 and region 2, respectively.

From equation (3.12) and some algebra the linear approximation matrix is

$$\boldsymbol{B} = \begin{pmatrix} Q_{1,1}\alpha_1 f_{1,1}\exp(-\beta_1 N^*_{0,1}) & Q_{2,1}\alpha_1 f_{2,1}\exp(-\beta_1 N^*_{0,1}) & Q_{1,1}\alpha_1 f_{1,1}\exp(-\beta_1 N^*_{0,1}) & 0 & 0 & 0 \\ S_{1,1}\theta_1(1-1) & 0 & 0 & S_{1,1}\theta_1(2-1) & 0 & 0 \\ 0 & S_{2,1}\theta_2(1-1) & 0 & 0 & S_{2,1}\theta_2(2-1) & 0 \\ 0 & 0 & 0 & Q_{1,2}\alpha_2 f_{1,2}\exp(-\beta_2 N^*_{0,2}) & Q_{2,2}\alpha_2 f_{2,2}\exp(-\beta_2 N^*_{0,2}) & Q_{1,2}\alpha_2 f_{1,2}\exp(-\beta_2 N^*_{0,2}) \\ S_{1,2}\theta_1(1-2) & 0 & 0 & S_{1,2}\theta_1(2-2) & 0 & 0 \\ 0 & S_{2,2}\theta_2(1-2) & 0 & 0 & S_{2,2}\theta_2(2-2) & 0 \end{pmatrix}$$

where $Q_{a,i} = 1 - \beta_i f_{a,i} N^*_{a,i}$. Incorporating the parameter values we obtain

$$\boldsymbol{B} = \begin{pmatrix} 0.124 & 0.187 & 0.160 & 0 & 0 & 0 \\ 0.516 & 0 & 0 & 0.430 & 0 & 0 \\ 0 & 0.656 & 0 & 0 & 0.246 & 0 \\ 0 & 0 & 0 & 0.082 & -0.064 & -0.082 \\ 0.316 & 0 & 0 & 0.395 & 0 & 0 \\ 0 & 0.148 & 0 & 0 & 0.518 & 0 \end{pmatrix}.$$

The eigenvalues λ_i and magnitudes $|\lambda_i|$ of $\boldsymbol{B}$ are

λ_i	$\lvert\lambda_i\rvert$
0.4988	0.4988
-0.1821 + 0.2581i	0.3159
-0.1821 - 0.2581i	0.3159
0.1044 + 0.1699i	0.1994
0.1044 - 0.1699i	0.1994
-0.1372	0.1372

Since the magnitudes of all the eigenvalues of $\boldsymbol{B}$ are < 1.0, the equilibrium population is stable. Also, there are some negative eigenvalues. Thus, the population cycles after a perturbation from the equilibrium as was observed in Figure 3.1.

The complex behavior that the model is capable of exhibiting is illustrated in Figure 3.2. Here we change early life survival α_i from 0.20 to 0.70 for α_1 and from 0.15 to 0.60 for α_2. Based on visual examination, the population appears to exhibit quasi-periodic dynamics where there appears to be a repetitive pattern (Caswell 1989; Nisbet and Gurney, 1982). Again most of the behavior of the population was due to fluctuations among age classes (Figure 3.2). The regional distribution exhibits small fluctuations.

Application to Sablefish

Traditional Leslie Matrix With Migration

Sablefish, one of the most valuable commercial fish in waters off Alaska, is used to illustrate the application of the model. Migration rates based on tagging experiments have been estimated by Heifetz and Fujioka (1991 [chapter 1]). Population parameters and age-specific migration rates are shown in Tables 3.1 and 3.2, respectively. There are five regions which correspond to the five North Pacific Fishery Management Council (NPFMC) regulatory areas. Note that the population parameters are assumed to be the same in reach region. Estimates of egg production and number of recruits at age 3 are derived from the results of an age-structured stock assessment of Alaska's sablefish population (Sigler, 1993; updated by M. Sigler personal communication, October 1995). This age-structured model includes observations of relative abundance, age composition and size composition from the Japan-US cooperative longline survey and commercial catch data. The model provides estimates of numbers at age for the sablefish population pooled over regions during 1976 - 1995.

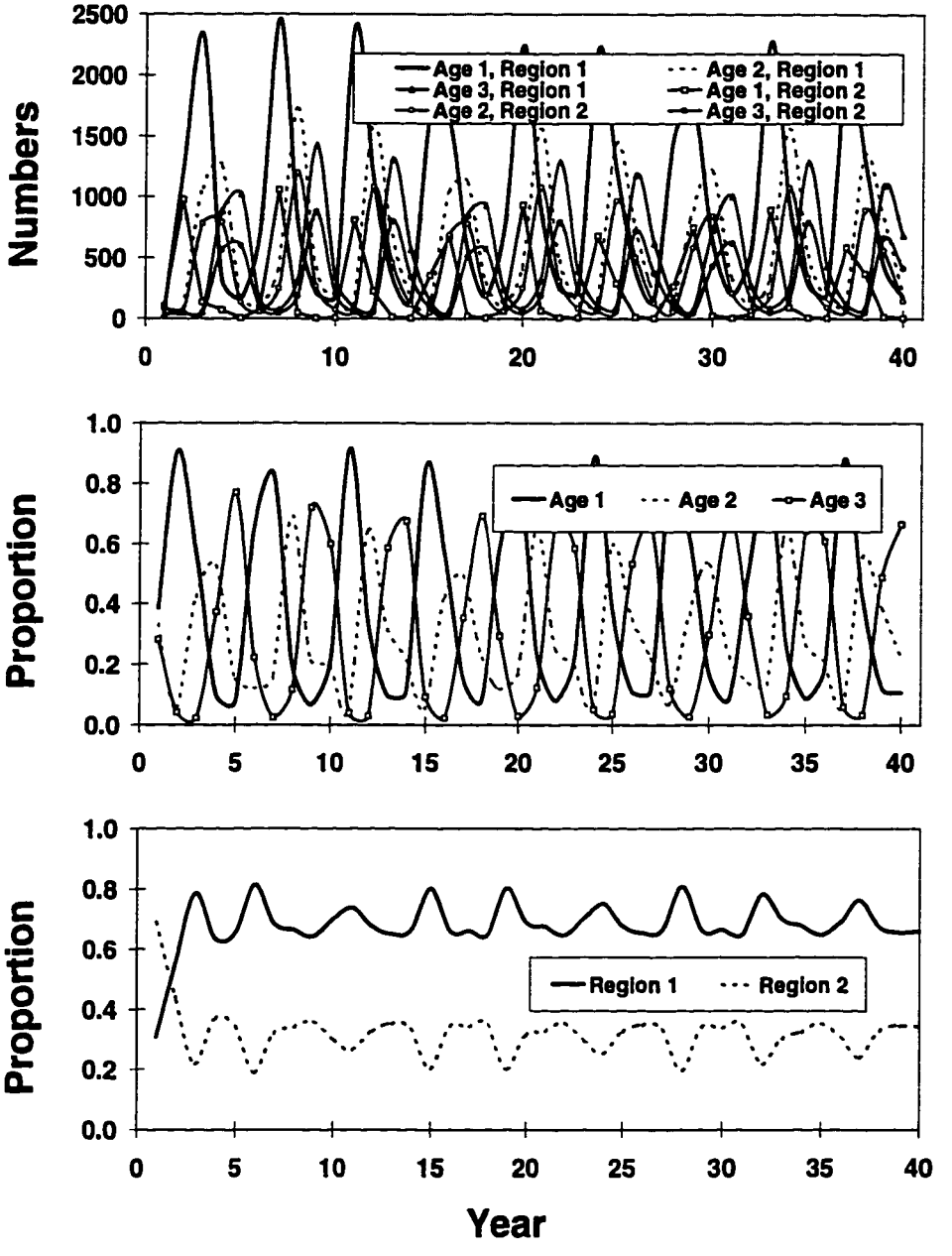

Figure 3.2. Projection of a hypothetical fish population based on the age-by-region model with density dependence defined with $(\alpha, \beta) = (0.70, 0.0001)$ and (0.60, 0.0002) for region 1 and region 2, respectively.

Table 3.1. Estimates of population parameters for sablefish in the northeastern Pacific Ocean. Fraction mature, selectivity at age, and growth parameters are from Sigler and Fujioka (1993). Fecundity parameters are adapted from Lowe *et al.* (1991).

Age (a)	3	4	5	6	7	8	9	10	11	12	≥ 13
Natural mortality M	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10
Maturity (m_a)	0.002	0.032	0.232	0.629	0.868	0.949	0.977	0.988	0.993	0.998	1.00
Selectivity (s_a)	0.15	0.32	0.48	0.63	0.73	0.82	0.88	0.93	0.97	1.00	1.00

Female von Bertalanffy length - age model	Female allometric weight-length model	Fecundity model
$L_a(cm) = L_\infty(1-exp(-k(a-t_0)))$	$weight_a\,(kg) = cL_a^b$	$f_a(eggs) = m_a 0.02349(L_a)^{3.88}$
$L_\infty = 81.4$	$c = 3.15 \times 10^{-6}$	
$k = 0.249$	$b = 3.290$	
$t_0 = -0.770$		

Annual estimates of egg production were determined from the product of net fecundity at age and numbers at age

$$N_{0,t} = 0.5\sum_{a=3}^{A} f_a N_{a,t} ,$$

where "0.5" represents the assumption that half the fish at each age are female. Our estimates of annual egg production, recruitment, and early life survival are shown in Table 3.3. The median early life survival of 1.00×10^{-6} from Table 3.3 can be used as an estimate of l_r (Quinn and Szarzi, 1993).

To initialize the population we estimated the regional age composition of the population in 1991. The age composition in 1991 is based on ageing otoliths from fish collected during the 1991 Japan-US Cooperative longline survey. The most recent year where age data were collected from all NPFMC regulatory regions was 1991. The raw age composition data were divided by selectivity at age from Table 3.1 and converted to proportions $p_{a,i}$ within a region. Given survey estimates of relative population numbers by region (RPN's) and total population numbers (N_t) from the age structured model, region (RPN's) and total population numbers (N_t) from the age structured model,

population abundance at age and region at t = 1991 was estimated from

$$N_{a,t,i} = \frac{N_t p_{a,i} RPN_{t,i}}{\sum_{i=1}^{5} RPN_{t,i}} .$$

Table 3.2. Annual movement rates from one area to another for different age groups of sablefish; adapted from Heifetz and Fujioka (1991[chapter 1]).

From	To area (k)				
area (i)	EG	CG	WG	BS	AL
Age 3-4					
EG	0.489	0.378	0.109	0.012	0.012
CG	0.194	0.484	0.229	0.047	0.046
WG	0.078	0.322	0.308	0.145	0.147
BS	0.010	0.073	0.160	0.710	0.047
AL	0.005	0.040	0.093	0.049	0.813
Age 5-8					
EG	0.712	0.227	0.054	0.003	0.004
CG	0.273	0.476	0.199	0.023	0.029
WG	0.134	0.409	0.285	0.072	0.100
BS	0.029	0.165	0.246	0.494	0.066
AL	0.013	0.077	0.128	0.034	0.748
Age ≥ 9					
EG	0.751	0.200	0.044	0.002	0.003
CG	0.472	0.426	0.074	0.011	0.017
WG	0.262	0.116	0.517	0.046	0.059
BS	0.095	0.181	0.259	0.287	0.178
AL	0.047	0.103	0.155	0.018	0.677

EG, Eastern Gulf of Alaska; CG, Central Gulf of Alaska; WG, Western Gulf of Alaska; BS, Eastern Bering Sea; AL, Aleutians.

Table 3.3 Stock and recruitment data for sablefish in the northeast Pacific Ocean. Estimates of egg production and number of recruits at age 3 are derived from the results of an age-structured stock assessment of Alaska's sablefish population (Sigler, 1993; updated by M. Sigler personal communication, October 1995).

Year	Eggs (10^{12})	Recruitment at age 3 (10^{6})	Survival to age 3 (10^{-6})
1976	7.09	23.09	3.26
1977	7.05	44.19	6.27
1978	7.61	40.60	5.33
1979	8.57	31.09	3.62
1980	8.95	38.01	4.25
1981	9.50	41.70	4.39
1982	10.87	13.82	1.27
1983	13.41	15.25	1.14
1984	16.41	14.27	0.87
1985	19.23	10.10	0.53
1986	21.94	5.05	0.23
1987	23.64	5.16	0.22
1988	23.78	4.15	0.17
1989	22.70	4.49	0.20
1990	21.35	8.69	0.41
1991	19.63	4.57	0.23
		median =	1.00

During 1992 - 95 the transition matrix $\boldsymbol{P}$ is applied with F rates from Sigler (personal communication, October 1995). These F rates were 0.088, 0.094, 0.111, and 0.105 for 1992-1995, respectively. Projection of future abundance starting in 1996 is made with the F value (F_{st}) that results in stationary population abundance (i.e., $\lambda_1 = 1$). The F_{st} value of 0.143 was determined with a nonlinear search procedure.

The projected population reaches a stable age-by-region equilibrium in about 25 years (Figure 3.3 and 3.4). The initial dip in numbers of age > 10 sablefish is due to the poor recruitment in recent years (Figure 3.3). The regional distribution stabilized in about

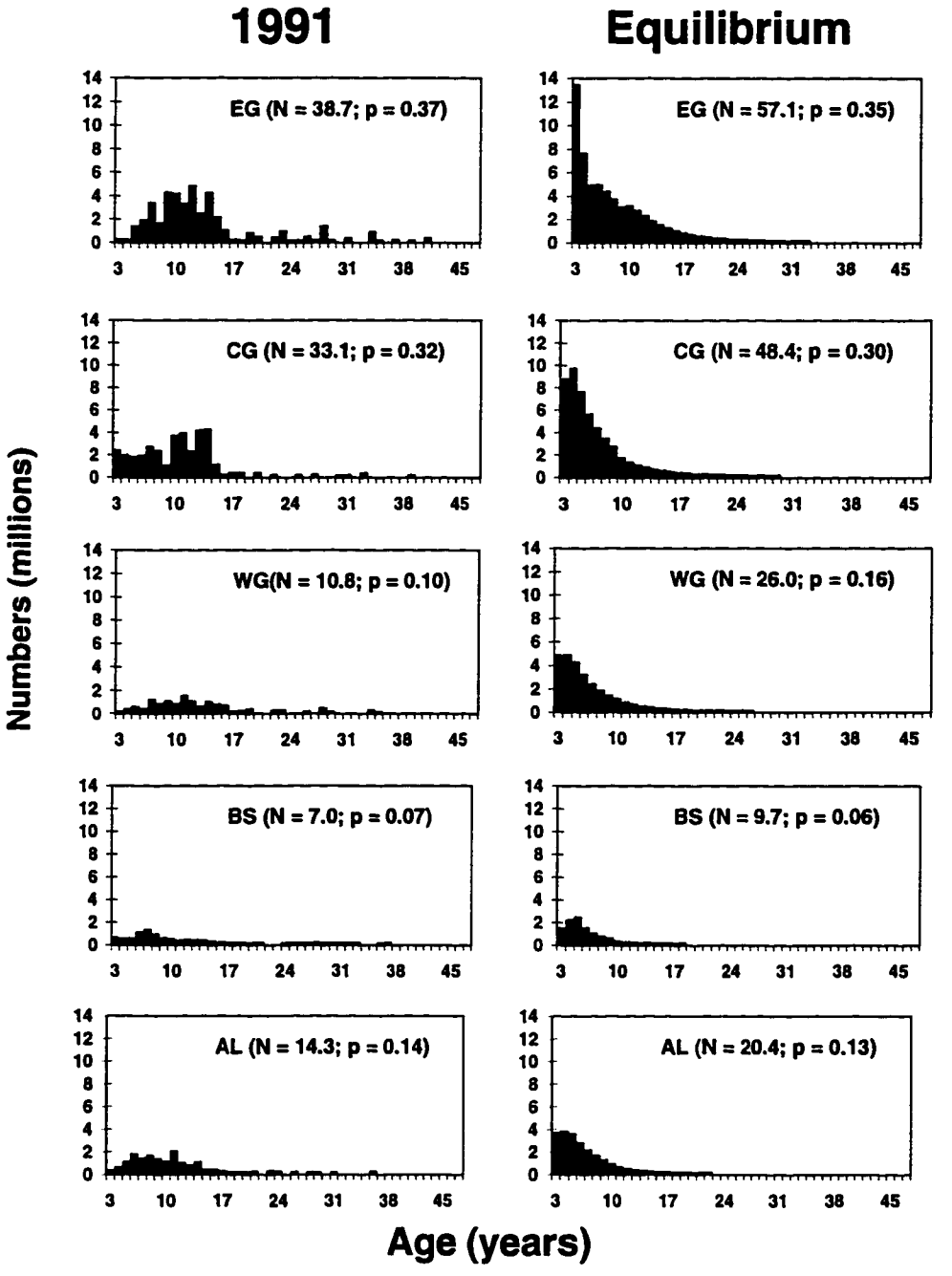

Figure 3.3. Estimated age composition of sablefish by region in 1991 and equilibrium age composition by region based on the traditional Leslie matrix with migration, median early life survival of 1.00 X 10^{-6}, and F_{st} = 0.143. N = population numbers by region and p = proportion of total population by region. EG, Eastern Gulf of Alaska; CG, Central Gulf of Alaska; WG, Western Gulf of Alaska; BS, Eastern Bering Sea; AL, Aleutians.

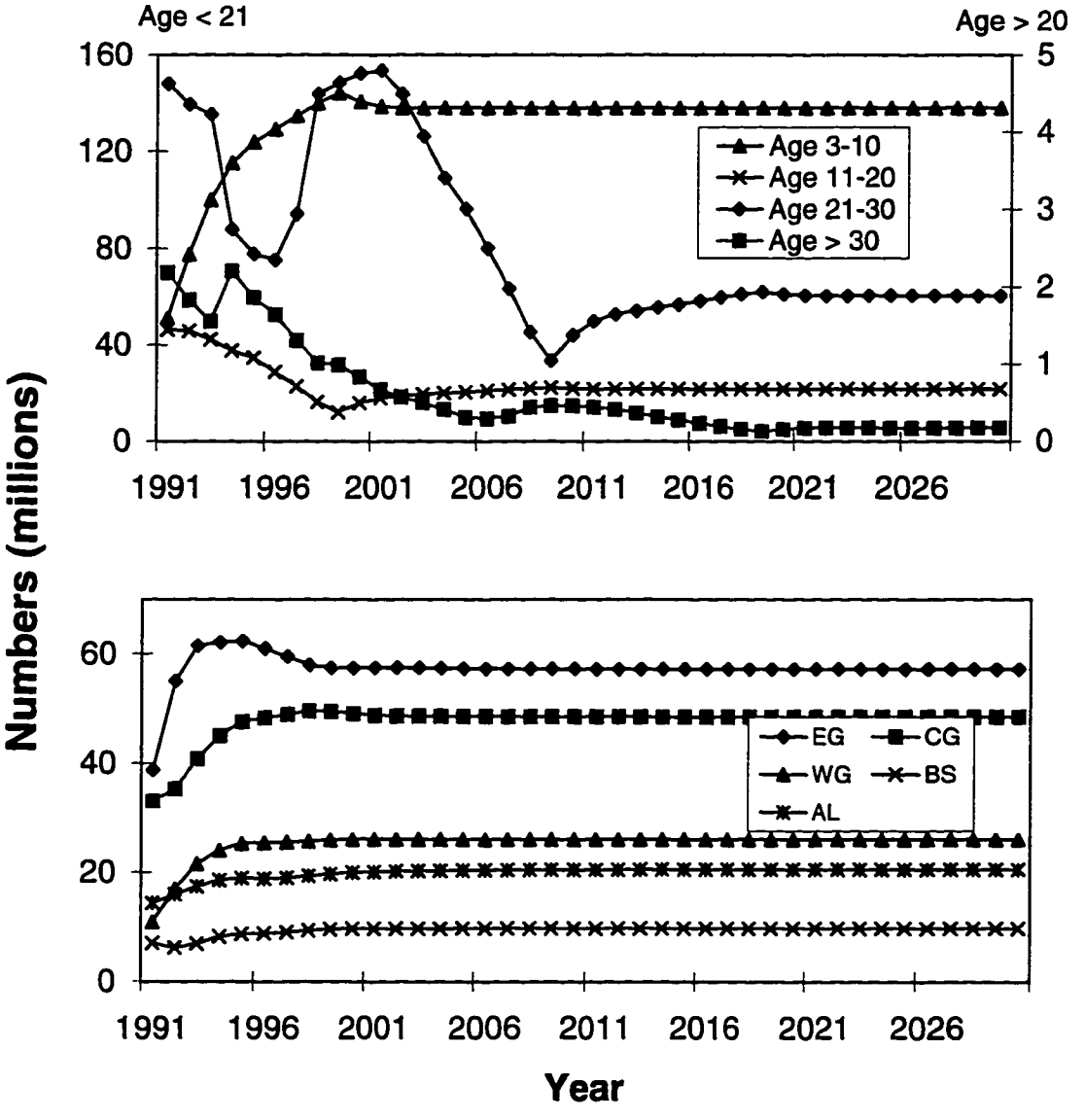

Figure 3.4. Estimated abundance of sablefish by age and region from 1991 - 1995 and projected abundance from 1996 - 2031 based on the traditional Leslie matrix approach with migration, median early life survival of 1.00 X 10^{-6}, and F_{st} = 0.143. EG, Eastern Gulf of Alaska; CG, Central Gulf of Alaska; WG, Western Gulf of Alaska; BS, Eastern Bering Sea; AL, Aleutians.

5 years which was much faster than the age distribution. Thus for sablefish, the amount of mixing among regions is rapid relative to the progression of a cohort through the age classes. This is partly due to sablefish being long lived, the considerable time for the initial population to die out, and that additions to the overall population are only made at the youngest age. On the other hand, movement is rapid; annually 19-72% of the population in a region migrates to other regions and exchange occurs among all regions. The damping ratio ρ for the projection matrix was 1.272.

To examine the influence migration rates have on the convergent properties of the population we examined the sensitivity of the damping ratio ρ to incremental changes in migration rates. Migration rates given in Table 3.3 are hereafter termed baseline migration rates. The sensitivity to migration rates was assessed by increasing or decreasing all baseline $\theta(i \rightarrow k)$ values (for $i \neq k$) a given percentage then adjusting the baseline $\theta(i \rightarrow i)$ values to assure that $\sum_{k=1}^{K} \theta_{a,l}(i \rightarrow k) = 1$. Thus an increase in $\theta(i \rightarrow k)$ values results in an increase in amount of migration out of an area.

All of the populations described in Table 3.4 will grow at the same rate because λ_1 is the same for all the populations, but there may be differences in the regional population distribution and rate of convergence to the stable distribution. Increasing the amount of migration resulted in essentially no change in ρ, whereas decreasing migration resulted in considerable reduction in ρ (Table 3.4). This limited sensitivity analysis indicates that speed of convergence for baseline migration rates is at or near the maximum possible given the other parameters of the model.

Table 3.4. Sensitivity of the damping ratio ρ to changes in migration rates.

Change in $\theta(i-k)$ values (%)	damping ratio ρ
40	1.2721
20	1.2721
0 (baseline)	1.2721
-20	1.2206
-40	1.1566
-60	1.0991
-80	1.0471

Based on Table 3.4 we characterize migration rates as *fast* for a damping ratio of 1.272 corresponding to the baseline migration rates and *slow* for a damping ratio of 1.047 corresponding to a change in baseline $\theta(i-k)$ values of -80%. The regional abundance converged in about 25 years for slow migration rates compared to 5 years for fast migration rates (Figure 3.5). There was no difference between slow and fast migration rates in the rate of convergence of the age distribution.

Density Dependence

To introduce density dependence, egg production and subsequent recruits from Table 3.3 can be used to estimate a stock-recruitment relationship. When plotted, the data are suggestive of a Ricker type relationship (Figure 3.6) of the form

$$N_{r,t-r} = \alpha N_{0,t} exp(-\beta N_{0,t}) . \qquad (3.13)$$

Parameters for equation (3.13) were estimated using a nonlinear search procedure available in EXCEL spreadsheet software.

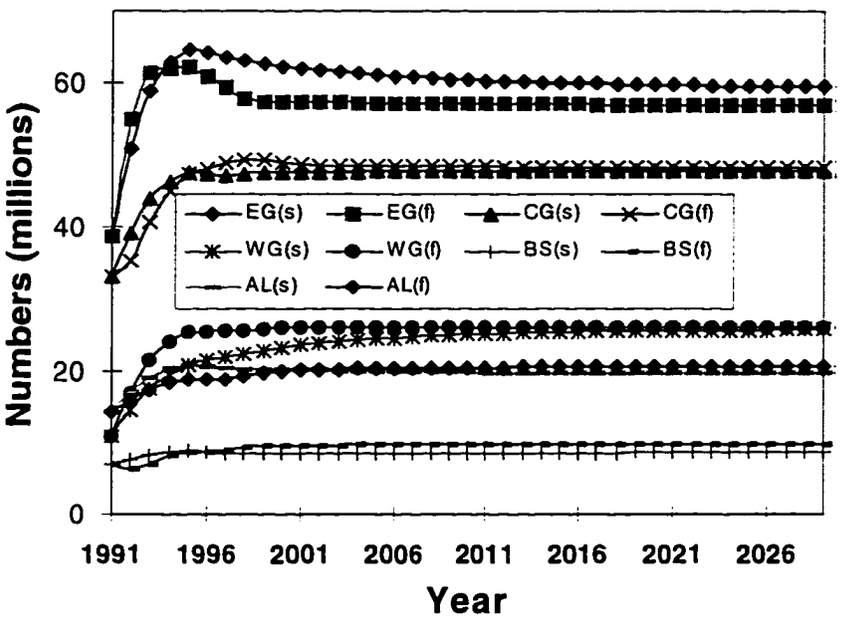

Figure 3.5. Comparison of the rate of convergence of the regional distribution of sablefish for slow (s) and fast (f) migration rates based on the traditional Leslie matrix approach with migration, median early life survival of 1.00 X 10^{-6}, and F_{st} = 0.143.

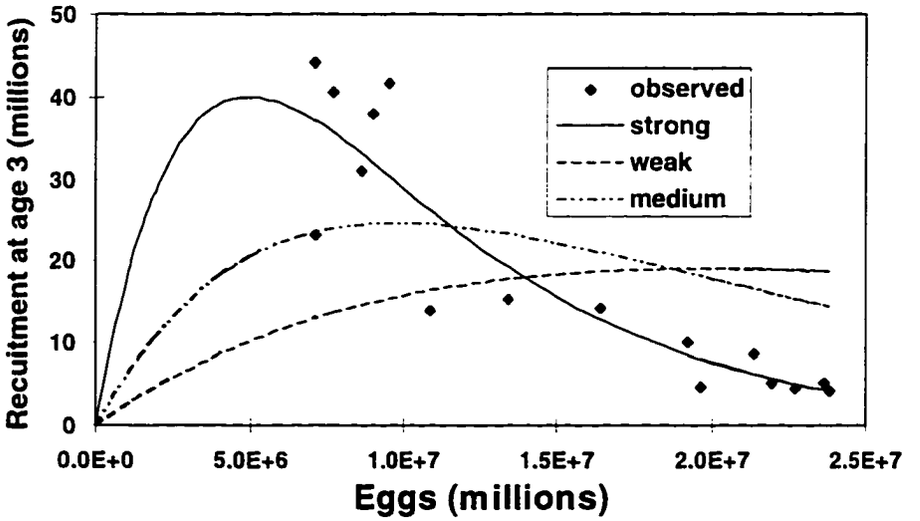

Figure 3.6. Observed recruitment versus egg production and three Ricker stock-recruitment curves for sablefish in Alaska. Strong, medium, and weak density dependence are defined with (α, β) = (2.21 X 10^{-5}, 2.04 X 10^{-7}), (6.86 X 10^{-6}, 1.02 X 10^{-7}), and (2.65 X 10^{-6}, 5.09 X 10^{-8}).

The best fit to the data are with parameter values of 2.214×10^{-5} for α and 2.037×10^{-7} for β. Such a fit indicates an extremely strong level of density dependence and is probably unrealistic (Figure 3.6). Thus, the stock-recruitment relationship is mainly used for illustrative purposes. Given the large uncertainty in this relationship, alternative levels of density dependence that are reasonably consistent with the data are based on values of β one-half (medium density dependence) and one-quarter (weak density dependence) the best fit estimate of β (Figure 3.6). The results with medium density dependence (ie., $\alpha = 6.86 \text{ X } 10^{-6}$; $\beta = 1.02 \text{ X } 10^{-7}$) are used to illustrate the application of the model.

The population was initialized with the estimated 1991 population and projected with $F = 0.1$ (near the current level). Figure 3.7 shows the trajectories of population number by region for a medium level of density dependence for fast and slow migration rates. In general the approach to the equilibrium population was a succession of damped oscillations. Slow migration rates tended to result in a higher proportion of the equilibrium population in the EG compared to fast migration rates. We also initialized the population with alternate starting population sizes and regional distributions. In all instances the population converged to the same location. We also verified this result by computing eigenvalues of the linear approximation matrix. Thus for the parameter values examined there exists a locally stable equilibrium.

As with the hypothetical example, certain parameter values can cause instability of the equilibrium population. For example in Figure 3.8, α in one region (EG) was increased from $6.86 \text{ X } 10^{-6}$ to $1.00 \text{ X } 10^{-3}$. The resulting regional population numbers exhibit undamped oscillations with periodic shifts in the proportion of the population in each region. An interesting cyclical occurrence is the periodic, nearly equivalent population numbers in EG and CG accompanied by the peak in the proportion of the population in the other regions.

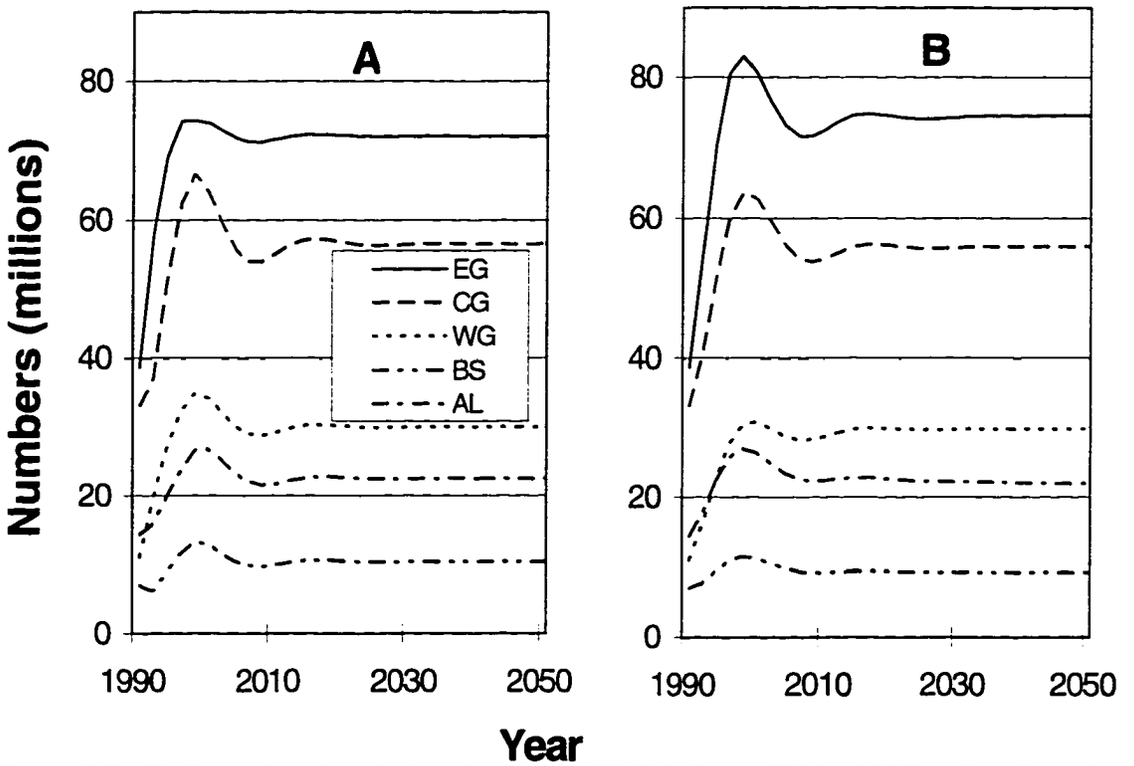

Figure 3.7. Estimated regional abundance of sablefish from 1991 - 1995 and projected abundance from 1996- 2031 with $F = 0.1$ and Case 1 of density dependence defined by a Ricker stock-recruitment relationship with $(\alpha, \beta) = (6.86 \times 10^{-6}, 1.02 \times 10^{-7})$. A = fast migration rates; B = slow migration rates.

Management Application: Per-recruit analysis

The age-by-region model can be easily adapted to examine harvest strategies. Based on the traditional Leslie matrix approach, a fishing rate can be devised that results in the projected population meeting a specific criterion. For example, fishing at a constant rate among regions $\leq F_{st}$ keeps the population at or above current levels. Alternatively, if a stock-recruitment relationship can be defined, a level of harvest can be devised to maximize sustainable yield. For most commercial fisheries there is great difficulty in reliably defining the stock-recruitment relationship. Per-recruit analysis is frequently used when there is uncertainty in the stock-recruitment relationship (Clark, 1991). Thus our management application of the model focuses on per-recruit analysis.

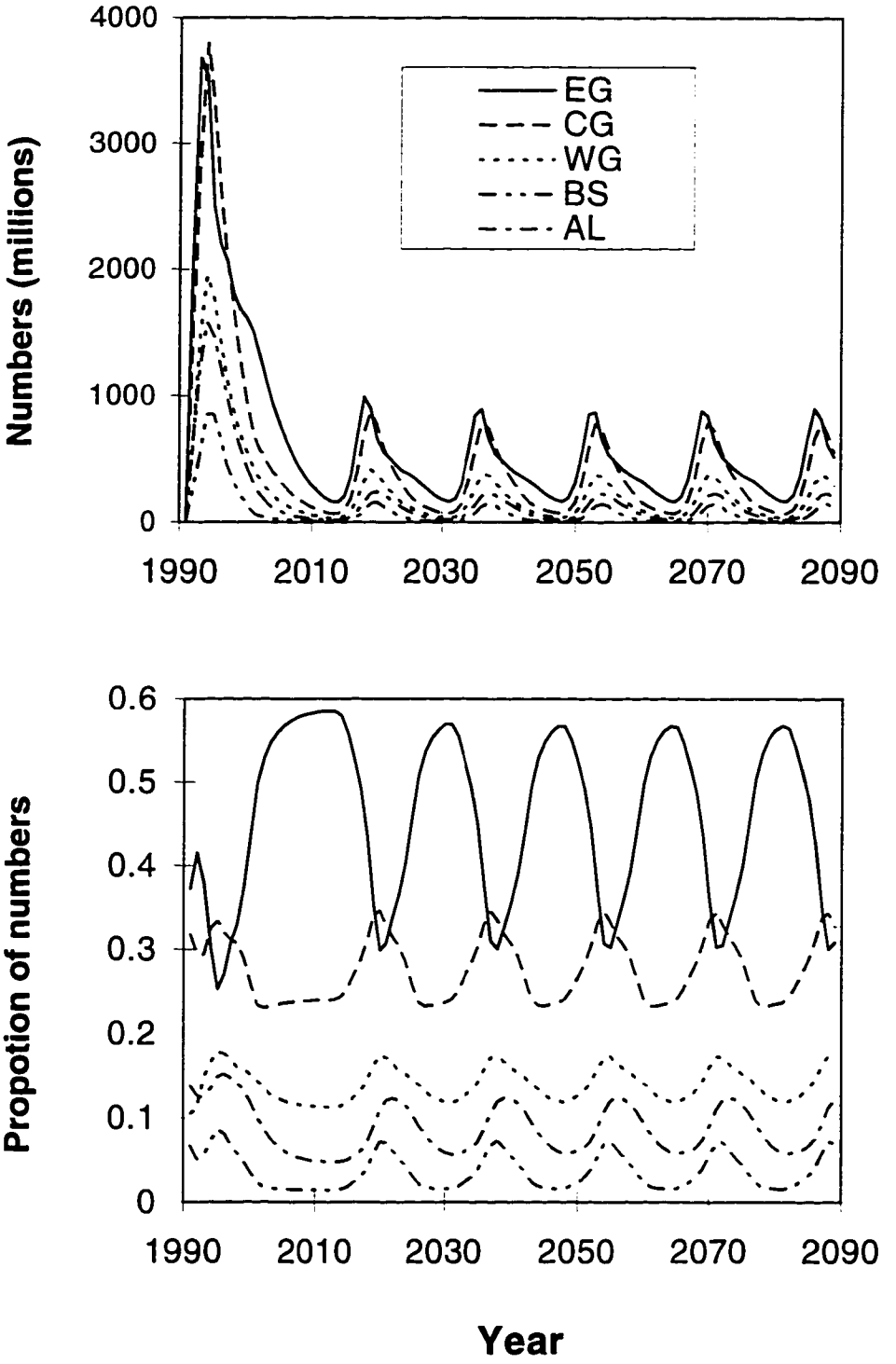

Figure 3.8. Estimated regional abundance and regional distribution of sablefish from 1991 - 1995 and projected abundance from 1996- 2031 with $F = 0.1$ and Case 1 of density dependence defined by a Ricker stock-recruitment relationship with $(\alpha, \beta) = (6.86 \text{ X } 10^{-6}, 1.02 \text{ X } 10^{-7})$ and $\alpha_{EG} = 1.00 \text{ X } 10^{-3}$.

In per-recruit analysis, the consequences of fishing are surmised from following a cohort as it passes through the fishery during its life-span. By rewriting equations (3.2) and (3.4) as a series of equations to be updated, per recruit analyses can be undertaken. Given initial and perhaps arbitrary recruitment numbers by region ($N_{r,i}$), the abundance for each age and region after migration can then be written as

$$N'_{a,i} = \sum_{k=1}^{K} \theta_a(k \to i) N_{a,k} \quad for a > r. \qquad (3.14)$$

The catch at age and region is

$$C_{a,i} = \mu_{a,i} N'_{a,i} , \qquad (3.15)$$

and the updated abundance at age after movement and survival is

$$N_{a+1,i} = S_{a,i} N'_{a,i} . \qquad (3.16)$$

One example of an initial recruitment vector is to start with 1,000 recruits per region. Another is to distribute them in proportion to estimates from a survey or stock assessment. Catch, yield (Y), and spawning biomass (SB) per recruit can be computed from

$$\frac{C_i}{N_r} = \frac{\sum_{a=r}^{A} \mu_{a,i} N'_{a,i}}{N_r}$$

$$\frac{Y_i}{N_r} = \frac{\sum_{a=r}^{A} \mu_{a,i} N'_{a,i} w_{a,i}}{N_r}$$

$$\frac{SB_i}{N_r} = \frac{\sum_{a=r}^{A} m_{a,i} N'_{a,i} w_{a,i}}{N_r}$$

where $w_{a,i}$ is weight at age and region and $m_{a,i}$ is the proportion mature at age and region. N_r, the total number of recruits for all regions combined, is used because recruitment from all regions may contribute to yield and spawning biomass within a given region. As shown in Heifetz *et al.* (1996 [chapter 2]), per recruit estimates can be sensitive to assumptions about the regional distribution of recruitment.

Another way of examining per recruit consequences is to follow an individual cohort from a region and keep track of the catch, yield, and spawning biomass by region during the cohort's lifetime. This is accomplished by starting with arbitrary $N_{r,i}$ for an individual region and using equations (3.14) - (3.16) to keep track of the population throughout a cohort's lifetime.

Commonly used reference fishing mortality rates such as F_{max}, $F_{0.1}$ and $F_{35\%}$ (Clark, 1991), can be determined for each region and all regions combined. The use of F_{max}, the F value that maximizes yield per recruit, has mostly passed out a favor because this rate is typically very high and will likely deplete spawning biomass too drastically (Clark, 1991). We present F_{max} values, however, because they are useful benchmarks for comparing among regions. $F_{0.1}$ is the rate where the slope of the yield per recruit curve as a function of F falls to 10% of the value at the origin. $F_{35\%}$ is the rate required to keep spawning biomass per recruit at 35% of the unfished level. For sablefish $F_{0.1}$ is close to $F_{35\%}$, and $F_{35\%}$ is the current harvest strategy (Fujioka, 1995). Thus, only results for F_{max} and $F_{35\%}$ are shown.

We examine two management applications of the model based on per-recruit analysis. The implications for fishery management are first examined with a constant fishing rate among regions. Second, we show how regional specific fishing rates can be devised that result in the population in a given region meeting a specific criterion.

F Common Among Regions

To illustrate per recruit analysis we use the distribution of regional recruitment estimated with $F = 0$ based on the equations in the *traditional Leslie matrix with migration* section. Recruitment was distributed in the following proportions by region 0.439 in the EG, 0.270 in the CG, 0.146 in the WG, 0.039 in the BS, 0.106 in the AL.

We examine yield per recruit (YPR) and spawning biomass per recruit (SBPR) as a function of a common F among regions. YPR and SBPR expressed relative to the maximum within a region are shown in Figure 3.9. The value of F that maximized YPR (F_{max}) differed dramatically by region. These F_{max} values are 0.20 for the EG, 1.02 for the CG, 0.86 for the WG, 1.44 for BS and 0.74 for the AL. Spawning biomass per recruit (SBPR) values also differed as a function of F by region. The values of F that reduced the SBPR to 35% of its unfished level ($F_{35\%}$) in a region were 0.09 for the EG, 0.12 in the CG, 0.13 in the WG, 0.20 in the BS, and 0.16 in the AL. The pooled $F_{35\%}$ value of 0.112 is the currently used exploitation strategy for sablefish in waters off Alaska. Fishing at the pooled rate will result in SBPR maintained at $\geq$ 35% of the unfished level for all regions except the EG.

The result that F values that maximize yields and maintain spawning biomass differ by region can be explained from the combination of two factors. The first factor is from differences in the rate at which abundance of a cohort changes with time due to "natural survival" (ie., the combination of natural mortality and migration). All other parameters being equal, in traditional YPR and SBPR analyses that do not consider migration, F_{max} and $F_{35\%}$ values are correlated with natural mortality M. The population with the greatest M will have the greatest values of F_{max} and $F_{35\%}$. For the age-region model, migration rates and natural mortality determine the level of natural survival of a cohort in a given region. This phenomenon is exemplified in Figure 3.10 which traces the relative abundance of cohort through time in each region in the absence of fishing. In general, the quicker the abundance declines in a region, the higher the F_{max} and $F_{35\%}$ values.

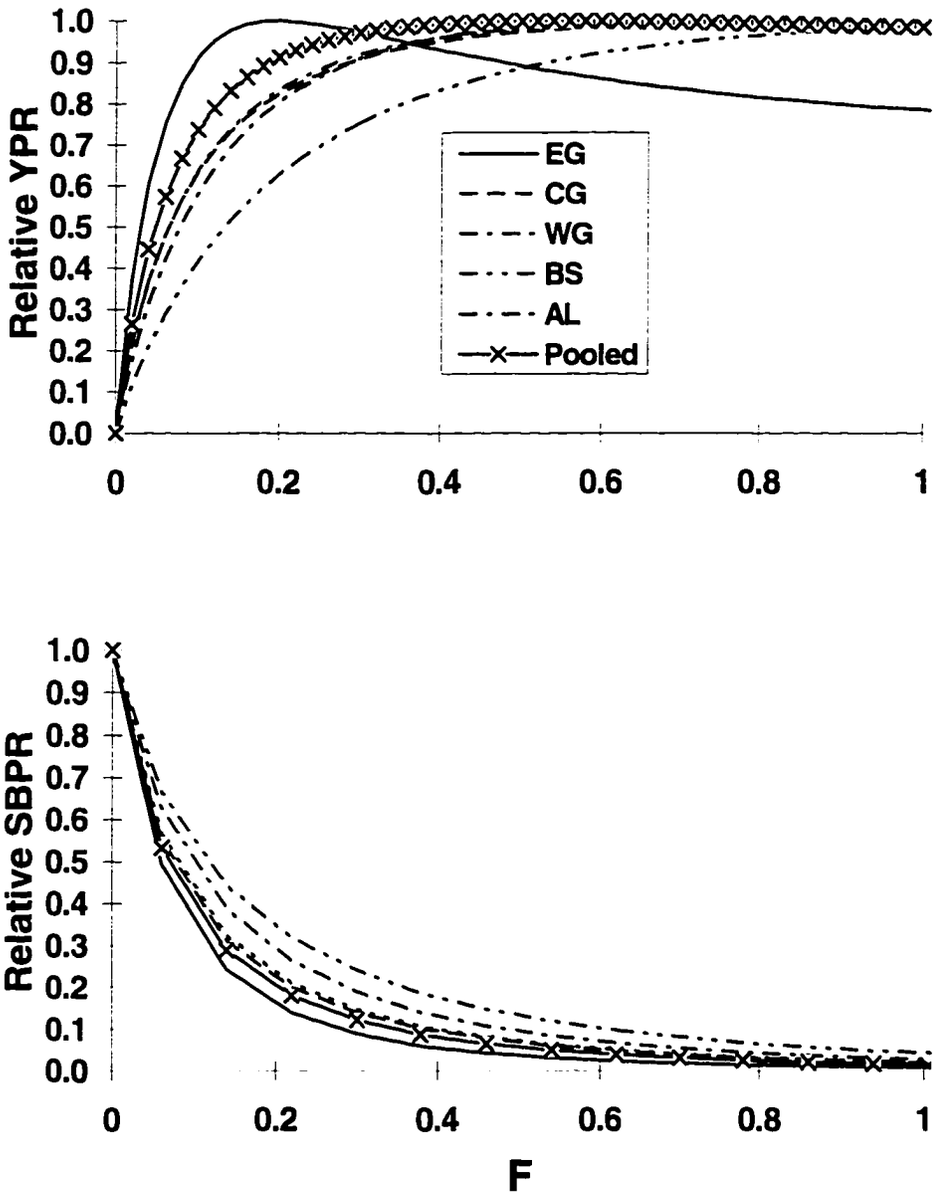

Figure 3.9. Yield per recruit (YPR) and spawning biomass per recruit (SBPR) relative to the maximum within a region for F common to all regions.

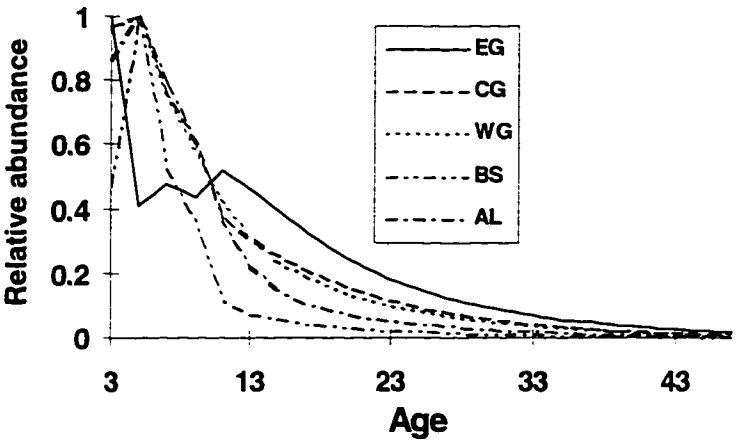

Figure 3.10. Abundance of cohort relative to the maximum in a region with $F = 0$.

The second factor that may influence per-recruit rates is fishery interceptions. For example, the lower value of F_{max} and $F_{35\%}$ in the EG compared to the other regions can in part be explained by the relationship between F and the regional distribution of yield and spawning biomass. As F increases an increasingly greater proportion of the yield is taken in other regions, especially in the CG (Figure 3.11). This phenomenon is paralleled for spawning biomass where an increasingly greater proportion of the spawning biomass is present in the CG as F is increased. Young sablefish (age 3-5) mostly migrate north and westward from the EG to other regions but return as they get older (Heifetz and Fujioka, 1991[chapter 1]).

Region-specific F

The results of the preceding section indicate that fishing at a constant rate that may be appropriate for the pooled population may be detrimental to the population in a given region. Alternatively there may be sets of region-specific fishing rates that meet fishery management goals. A fishery management goal can be formulated as an objective

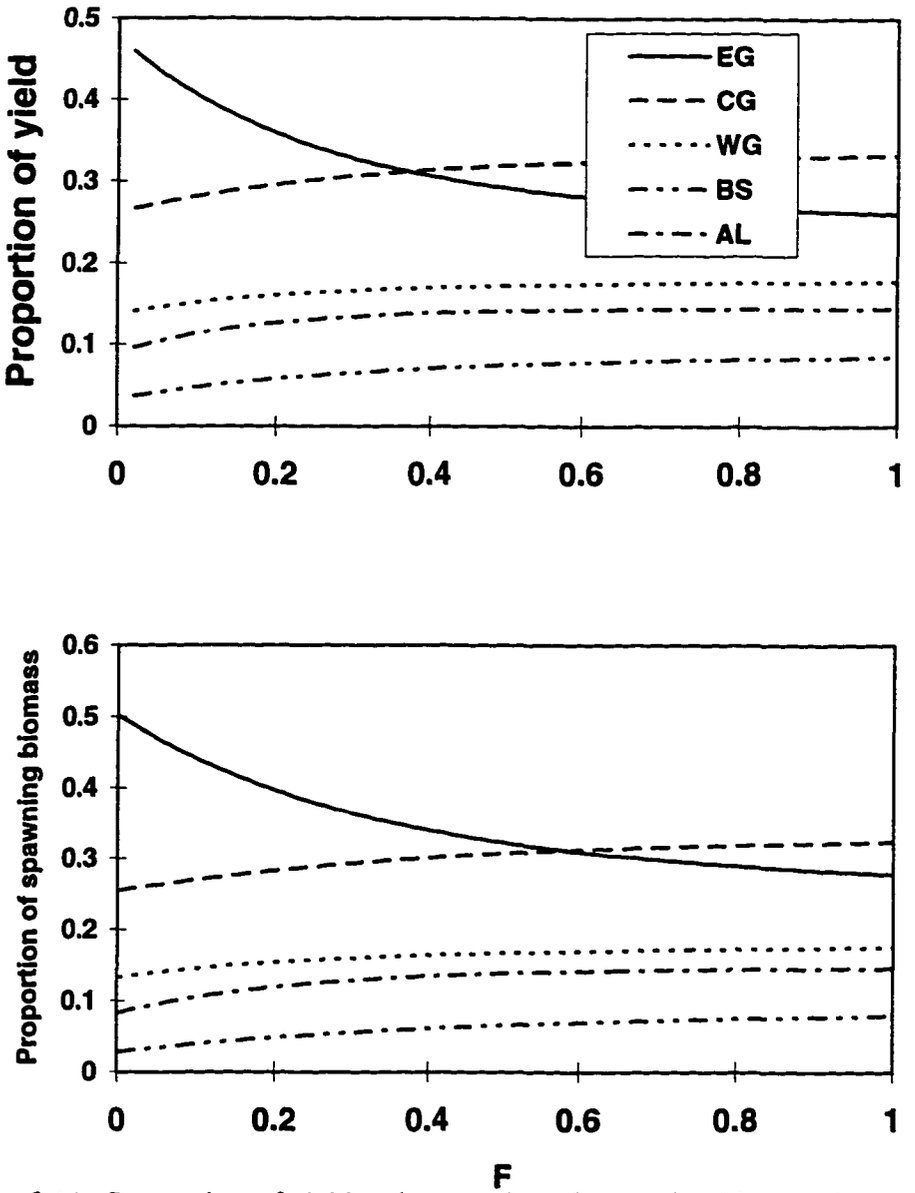

Figure 3.11. Proportion of yield and proportion of spawning biomass by region versus *F*.

function to be optimized. For example, a reasonable goal of fishery management might be to choose a set of region-specific F values that maintain the regional distribution of spawning potential at unfished levels and at the same time maintain pooled spawning biomass per recruit at a specified target level. The objective function for such a goal comprises two parts: 1) the sum over regions of the squared deviations between regional-specific proportions of spawning biomass (SBP) with and without fishing and, 2) the squared deviation between the reduction in pooled spawning biomass per recruit (SBPR) relative to unfished levels and a target level of reduction (x),

$$\min \left[\sum_{i=1}^{I} \left(SBP_{F_i} - SBP_{F_i=0} \right)^2 + \left(\frac{\sum_{i=1}^{I} SBPR_{F_i}}{\sum_{i=1}^{I} SBPR_{F_i=0}} - x \right)^2 \right].$$

To illustrate this approach for sablefish, we set the target level of reduction for SBPR at 35% of the unfished level (ie., $x = 0.35$; Case 1 in Table 3.5). We also determined sets of F values that minimized the objective function given a fixed fishing rate (0.04 - 0.16) in a given region (EG) (Cases 2-5; Table 3.5). We used the distribution of regional recruitment based on $F = 0$ as determined in the *traditional Leslie matrix with migration* section. Recruitment was distributed in the following proportions by region 0.439 in the EG, 0.270 in the CG, 0.146 in the WG, 0.039 in the BS, 0.106 in the AL. Based on this distribution of recruitment equilibrium spawning biomass was distributed in the following proportions by region 0.502 in the EG, 0.254 in the CG, 0.133 in the WG, 0.028 in the BS, 0.083 in the AL. GAUSS program OPTMUM was used to determine the value of F for each region.

A target level of spawning biomass per recruit of 35% of the unfished level and regional preservation of the distribution of spawning biomass at unfished levels is

obtained at regionally specific F values (Case 1) that differ substantially from the constant regional $F_{35\%}$ value of 0.112 (Case 6; Table 3.5). Pooled yield was nearly identical for the constant F values and regional F values. The constant F value results in pooled spawning biomass per recruit meeting the target but disruption of the distribution of spawning biomass. An exact solution to the objective function was found at regional specific F values of 0.042 for the EG, 0.164 for the CG, 0.128 for the WG, 0.284 for the BS, and 0.180 for the AL. Thus relative to the constant F value the level of fishing would need to be reduced considerably in the EG, moderately increased in the CG, WG, and AL, and increased substantially in the BS to meet regional management goals. Analogous to the analysis of constant F values in the preceding section, differences in F values among regions can be explained from the influence of different natural survival rates among regions and fishery interceptions.

Fixing F for a variety of values for the EG and solving for the F values in the other regions shows the relationship among the regional F values (Cases 2-5; Table 3.5). In general as F_{EG} is increased, F values in the CG and WG decrease substantially while F values in the BS and AL remain relatively constant. While resulting in larger deviations in regional spawning distribution than the F values that optimized the objective function (Case 1), these sets of F values give some alternatives and consequences of adopting regionally specific harvest strategies.

Table 3.5. Regional F values, sum of squared deviations (SSQ), spawning biomass relative to unfished levels ($SBPR/SBPR_{F=0}$), spawning biomass (SB), proportion of spawning biomass (SBP), and yield.

Region	F	SSQ x 10^6	$SBPR/SBPR_{F=0}$	SB	SBP	Yield	
EG	0.042	0.01	0.350	32784	0.502	1886	Case 1
CG	0.164		0.350	16646	0.255	4519	
WG	0.128		0.350	8670	0.133	1829	
BS	0.294		0.350	1820	0.028	1169	
AL	0.180		0.350	5406	0.083	1755	
Pooled			0.350	65325		11158	
EG	0.040	6.19	0.351	32853	0.504	1781	Case 2
CG	0.168		0.348	16525	0.253	4623	
WG	0.130		0.348	8619	0.132	1855	
BS	0.291		0.351	1824	0.028	1157	
AL	0.179		0.350	5408	0.083	1745	
Pooled			0.350	65228		11161	
EG	0.080	1231.51	0.330	30915	0.475	3435	Case 3
CG	0.108		0.377	17932	0.276	3122	
WG	0.097		0.372	9219	0.142	1449	
BS	0.338		0.337	1749	0.027	1319	
AL	0.200		0.340	5256	0.081	1919	
Pooled			0.349	65072		11244	
EG	0.120	4907.24	0.310	29072	0.447	4965	Case 4
CG	0.060		0.403	19166	0.295	1810	
WG	0.070		0.395	9794	0.151	1091	
BS	0.355		0.338	1756	0.027	1394	
AL	0.216		0.336	5184	0.080	2059	
Pooled			0.348	64973		11318	
EG	0.160	10495.05	0.291	27263	0.421	6363	Case 5
CG	0.022		0.425	20189	0.312	684	
WG	0.049		0.416	10309	0.159	792	
BS	0.346		0.351	1827	0.028	1396	
AL	0.226		0.336	5185	0.08	2162	
Pooled			0.347	64773		11397	
EG	0.112	5652.76	0.303	28407	0.435	4521	Case 6
CG	0.112		0.372	17710	0.271	3216	
WG	0.112		0.387	9573	0.147	1738	
BS	0.112		0.504	2618	0.040	558	
AL	0.112		0.452	6984	0.107	1311	
Pooled			0.350	65292		11344	

Discussion

We have presented a general framework to model the regional dynamics of an age-structured fish population. The model has its origin in the generic stage-classified matrix model described in Caswell (1989). Compared to age-structured models that aggregate the populations in different regions, at a minimum the additional parameters needed to construct an age-by-region model are estimates of age-specific migration rates among regions. The model can accommodate dispersal patterns at early life stages and regional differences in the stock-recruitment relationship and demographic parameters. Data needed to incorporate such complexity are often not available for fish populations or may be difficult to collect, although for some species dispersal of early life stages is becoming better understood. Temporal and stochastic variation in model parameters can be incorporated to account for variability due to environmental or other extrinsic causes (e.g., Caswell, 1989; chapter 8). In cases where estimates of age-specific migration rates are not available, size rather than age can be used for stage classification (Caswell, 1989), or techniques based on stock-production models may be better suited (e.g., Die *et al.*, 1990; MacCall, 1990).

The age-by-region model can be modified to include a more complicated representation of migration dynamics such as density-dependent migration patterns. Such density-dependent migration patterns can result in damping of population cycles (Emlen, 1984). The "basin model" of MacCall (1990) incorporates density-dependent migration patterns but has not been extended to age-structured populations. An appealing feature of the basin model is the incorporation of possible interactions between population density, the geographic range of distribution of a population, and habitat suitability. Exploration of such an ecologically based model within the context of our model formulation might be warranted.

For some fish species inclusion of seasonal migration patterns may be required to adequately describe population dynamics. Examples of seasonal migrations are the

latitudinal shifts of many Mid-Atlantic Ocean fishes (e.g., bluefish [*Pomatomous saltatrix*]) related to seasonal changes in water temperature (Tyler, 1971; Colvocoresses and Musick, 1983) and the seasonal spawning migrations of Pacific whiting (*Merluccius productus*; Swartzman *et al.*, 1987), Atlantic cod (*Gadus morhua*; Rose *et al.*, 1995), and Pacific cod (*Gadus macrocephalus*; Shimada and Kimura, 1994) . To evaluate the interaction between seasonal migration and exploitation patterns may require that such migrations be included in the model structure. Accounting for seasonal changes in the fraction of the overall population that is available to fishing in a given region would require incorporation of an additional dimension to the model structure and a shorter time step.

Although Beverton and Holt (1957) and more recent studies such as Fujioka (1978), Polacheck (1990), Die *et al.* (1990), and Deriso *et al.* (1991) included spatial dynamics into their population models, most models used to describe the dynamics of exploited fish populations are based on the assumptions of a stock that is spatially homogeneous with uniform fishing mortality. We describe methods to examine the regional dynamics of an exploited fish population. These methods parallel those commonly used for a single stock or populations pooled over regions (Getz and Haight, 1989). The first method assumes there is a proportional relationship between stock size and recruitment. In the second method the assumption of a proportional relationship between stock size and recruitment is modified by inclusion of a stock-recruitment relationship that incorporates density dependence.

We described some of the theoretical aspects of incorporating various forms of a stock-recruitment relationship within an age-by-region model. Because of the flexibility of the model, extension of the theory to include such density dependence was reasonably straightforward. One of the most uncertain components of the dynamics of a fish population is the stock-recruitment relationship. In practice however, incorporation of additional complexity of regional specific stock-recruitment relationships in model

structure can make interpretation of results difficult. Models that assume no regional structure to the stock-recruitment relationship are more easily analyzed than age-by-region models. A balance between complexity and simplification is needed to insure that essential information is reasonably straightforward to extract yet biologically realistic.

Our application of the model focused on population projection and evaluation of harvest strategies. Other uses for the model include estimation of population abundance and parameters, environmental impact studies, and general ecological studies. An essential component of fisheries science is estimation of population abundance (i.e., stock assessment). For many species the method of obtaining regional estimates of abundance is by first obtaining the abundance of the population pooled over regions through age-structured modeling and then partition this estimate by regional specific estimates of relative abundance (i.e., fishery or survey catch per unit effort). Quinn *et al.* (1990) describe an alternative to this method called migratory catch-age analysis. The underlying equations that describe the dynamics of the population for their method are analogous to equations (3.1) and (3.2) in our formulation. Migration parameters were assumed to be known and were not estimated within the model. While generally improving the precision of regional estimates of abundance, a problem encountered was that negative abundance estimates occurred for some areas due to inconsistency of data sources or model deficiencies. To alleviate this problem perhaps migration rates could be determined within the estimation procedure, if sufficient data are available. Although adding complications to the estimation procedure, incorporation of estimation of migration rates into a stock assessment may improve estimates of stock abundance as was the case for Pacific whiting (Dorn *et al.*, 1990). For sablefish incorporation of tag data in the estimation procedure along with survey estimates of relative abundance may assure that regional estimates of abundance are consistent with the migratory character of the population.

Our management application of the model was used to show how a regional per-recruit analysis can be undertaken that enables estimates of reference harvest rates such as $F_{35\%}$ to be computed. This method is analogous to traditional per-recruit analyses that are commonly used when the stock-recruitment relationship cannot be defined (Clark, 1991). We applied the model to management of sablefish in the northeast Pacific Ocean. Although the model developed for sablefish was designed primarily as an exploration of the modeling approach, some implications for fishery management were demonstrated. When the age-by-region model was applied to sablefish, an analysis of the consequences of exploitation on regional population dynamics was possible. Fishing at a rate that may be appropriate for the pooled population may differentially affect the populations in each region. Region-specific harvest rates that are designed to maintain regional spawning potential are a major departure from the harvest strategy that is currently used to manage sablefish in Alaska. Adoption of region-specific harvest rates makes biological sense; however there is the potential for more conflicts among user groups if such fishing rates are used because individual quota shares are directly related to fishing rates. In addition, uncertainty in model parameters, especially movement rates (Heifetz and Fujioka, 1991 [Chapter 1]), was not incorporated into our analyses. Before a decision can be made whether or not to adopt regionally specific fishing rates, various alternative biological hypotheses and expected consequences may need to be identified. At the present time, the sablefish fishery is managed by individual fishing quotas (IFQ's) that are allocated by region. Adoption of the regional specific fishing rates would likely be met with strong resistance by some fisherman and embraced by others.

In conclusion, recognition of the importance of migration to the dynamics of exploited fish populations will enhance our understanding of how fisheries in different regions may interact with each other. We have presented a model framework that enables analysis of such populations. While not without pitfalls, especially with regard to data requirements, use of such a model may permit a reasonably realistic description of a

migratory fish population that can reveal dynamic processes that will otherwise be obscured.

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Summary and Conclusions

This study has focused on ways of analyzing and modeling the dynamics of a migratory fish population. The impetus for this study stemmed from the need to incorporate the migratory character of sablefish into the evaluation of harvest strategies. This provided an opportunity to develop a general framework to examine the regional dynamics of fish populations that enables implications for fisheries management to be addressed. Applying the techniques described in this thesis to other species may prove worthwhile.

A fundamental requirement for construction of a model of a migratory fish population is quantification of migration rates. In Chapter 1 the method of Hilborn (1990) is applied to estimate migration rates and their associated errors. Tagging data for other fish populations can likewise be analyzed by this method or other similar methods (e.g., Schweigert and Schwarz, 1993); however data requirements for application of these methods are demanding. If migration parameters are to be reliably estimated, tagged fish should be released over a number of years in all geographic areas with recoveries in all areas during the same time period. We were fortunate with sablefish because a large quantity of tags were systematically released in most geographic strata over a number of years with a reasonable number of recoveries from all areas in the commercial fishery. Others who wish to reliably estimate migration rates are encouraged to rigorously implement their tag release and recovery programs to ensure the highest quality data. Alternatively, crude information on migration rates may provide enough information to make some management decisions. If, for example, enough tag release and recovery data are available to conclude that migration among areas is very low then this may be enough to manage the populations as separate stocks.

Relative to sablefish in the northeast Pacific Ocean, results of Chapter 1 indicate that magnitude of annual sablefish migration out of an area was substantial; 19-72%

depending on fish size/age. The predominant direction of migration was eastward for large sablefish and westward for small sablefish. Some interesting questions that remain to be answered are what factors influence the propensity of sablefish to migrate and what is the year-to-year variability in migration patterns? Undoubtedly, for sablefish and other species, variability in oceanographic conditions may influence migration patterns, but density may also play a role. In addition, fish populations can contain subgroups for which migratory behavior is diverse. For example, females may have substantially different migration behavior than males, or fish that originate from a particular region may have a particular migration pattern. Examining such heterogeneity in migration patterns may increase our understanding of the migration process.

When an analyst has quantified migration rates and decided that they play an important role in the dynamics of a population, a logical next step is to examine management implications. In chapter 2 an age-structured model of the sablefish population that included migration, survival, and recruitment was constructed to examine yield-per-recruit and evaluate policies of regional apportionment of harvest. The concept of geographical yield-per-recruit was introduced to examine how fisheries in different regions may interact with each other. An important finding in this chapter was that the yield-per-recruit in a region is sensitive to assumptions about the geographic distribution of recruitment. By comparing the yield-per-recruit curve corresponding to each region, it is concluded that a fishing rate appropriate for the overall population can be detrimental to the population in a given region.

The method of apportionment based on the regional distribution of biomass is obviously correct for non-migratory populations with similar population parameters and is based on the assumption that populations in each region should be fished at a common rate. As shown in the geographical yield-per-recruit analysis there are some hazards to such a strategy due to the migratory nature of a population. However, given the observed variability in survey estimates of regional abundance and uncertainty about regional

recruitment dynamics and migration patterns, a policy of apportionment based on geographic distribution of estimated biomass that uses past observations as well as the current year is favored. Such a policy appears to be robust to migration dynamics and alternative assumptions about the geographical distribution of recruitment.

While simulation studies are a useful means to examine a particular problem at hand, in practice having a general model that can be applied to a variety of species and in different circumstances is desirable. In chapter 3 a generic age-by-region model that uses estimates of age-specific migration rates is formulated to study the dynamics of an age-structured population with migration. The use of matrix formulation provides a compact means to express the reproduction, mortality, and migration of a fish population and allows use of theoretical generalities to help explain the transient, equilibrium, and stability properties of such a population (Caswell, 1989). To apply such a model requires estimates of age-specific migration rates, and if available, estimates of region-specific reproductive and fishing rates. The versatility of the approach is exemplified by the description of methods to determine region-specific fishing rates for a fish population that preserve spawning potential on a regional basis. In this management application the interaction of fishing, natural mortality, and migration all played a role in determining regional spawning potential. This application represents an initial step in understanding how fisheries in different regions can interact with each other. Understanding regional aspects of the recruitment process (i.e., whether recruitment is a function of region-specific parameters) will be required to fully understand the implications of fishery effects on regional spawning potential.

The management of fisheries consists of the blending of stock assessment and decision making. At one end, stock assessment often involves a balancing between complexity and simplification to ensure that essential information is reliable, reasonably straightforward to extract, and biologically realistic. Often times, essential information includes estimates of fishing rates and stock sizes to recommend region-specific catch

quotas. Models can be constructed that capture all the intricacies of the dynamics of a population yet require enormous amounts of data to reliably estimate parameters. In most instances, incorporation of migration rates into a stock assessment model will add complexity and biological realism. At the other end, is decision making; given all the uncertainties in the stock assessment, what is the best catch quota? Are migration rates really needed to assess the population and make management decisions? The answer obviously depends on the particular circumstances.

This study has shown that incorporation of migration rates into a per-recruit analysis implies that region-specific exploitation rates are an appropriate harvest strategy for sablefish. The region-specific fishing rates that were computed are a logical extension of the fishing strategy advocated by Clark (1991) and used to recommend catch quotas for many groundfish species in the North Pacific Ocean and elsewhere. In Clark's procedure, a fishing mortality rate that reduces the spawning biomass per recruit to 35% of the unfished level was shown to obtain a high proportion of maximum sustainable yield over a range of life-history parameters and stock-recruit relationships. The approach to selecting a region-specific harvest strategy developed here requires the same life-history parameters used in Clark's procedure with the addition of age-specific migration rates. The region-specific fishing rates that are computed here are only appropriate for the hypothesis that regional recruitment strengths depend on region-specific spawning biomass. The analysis is thus an initial step in identifying a region-specific harvest strategy. A more in-depth study would need to consider alternative hypothesis about recruitment, perhaps within a decision analysis framework (Hilborn and Walters, 1992; Ianelli and Heifetz, 1995).

For sablefish as with many other species migration is not directly considered in the stock assessment process, although methods are available to incorporate migration into stock assessment via migratory catch-age-analysis (Quinn *et al.*, 1990). For sablefish and many other species regional estimates of abundance are obtained by first estimating

the abundance of the population pooled over regions through population modeling and then partitioning this estimate by region-specific estimates of relative abundance (i.e., fishery or survey catch per unit effort). As long as reliable estimates of region-specific relative abundance indices are available, then this method is adequate. This method however, does not foster understanding about why changes in regional population abundance occurs. In addition, integration of the migratory nature of a population into the stock assessment process enables estimation of regional recruitment strengths and may help assure that regional estimates of abundance are consistent with the migratory character of the population. Thus, to account for annual changes in regional abundance the migratory character of a population should be considered in the stock assessment and management decision process.

In conclusion, migration is a life-history aspect that is a fundamental character of many fish populations. This study has set the foundation for future development of procedures to realistically describe and sensibly harvest a migratory population. Studies designed to understand regional recruitment dynamics of migratory populations will hopefully be at the forefront of future research endeavors.

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